THE ORDOVICIAN TRILOBITE FAUNAS OF THE BUILTH-LLANDRINDOD INLIER, CENTRAL WALES. PART I

BY

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CONTENTS

SYNOPSIS

This paper is the first of a series in which the Ordovician trilobite faunas of the Builth-Llandrindod Inlier are to be described using biometrical techniques. The families Agnostidae, Raphiophoridae, Cheiruridae, Colpocoryphidae and Eohomalonotidae are described here and the following new species and subspecies erected: *Cnemidopyge parva*, *Flexicalymene aurora*, *Platycalymene tasgarensis* Shirley *simulata*, *Placoparina sedgwickii* (M'Coy) *shelvensis*. A short review of the stratigraphy and previous faunal studies is included, together with a general discussion on the use of biometrical techniques in trilobite studies.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE trilobites to be described in this series of papers are from the Ordovician rocks forming an inlier between the towns of Llandrindod Wells and Builth Wells[1] in the southern part of Radnorshire and the northern tip of Brecknock. The inlier, about nine miles long and five miles across at its widest point, is elongated from north-east to south-west (see Text-fig. 1). To the north-west the inlier appears to have a faulted contact with Ashgillian rocks which link the inlier to the main Ordovician outcrop of Central Wales. Little research has been done on that region and it is beyond the scope of this work.

The relationship between this inlier and the other Ordovician outcrops of Wales and the Borderlands is shown in Text-fig. 2. From this it is apparent that the inlier

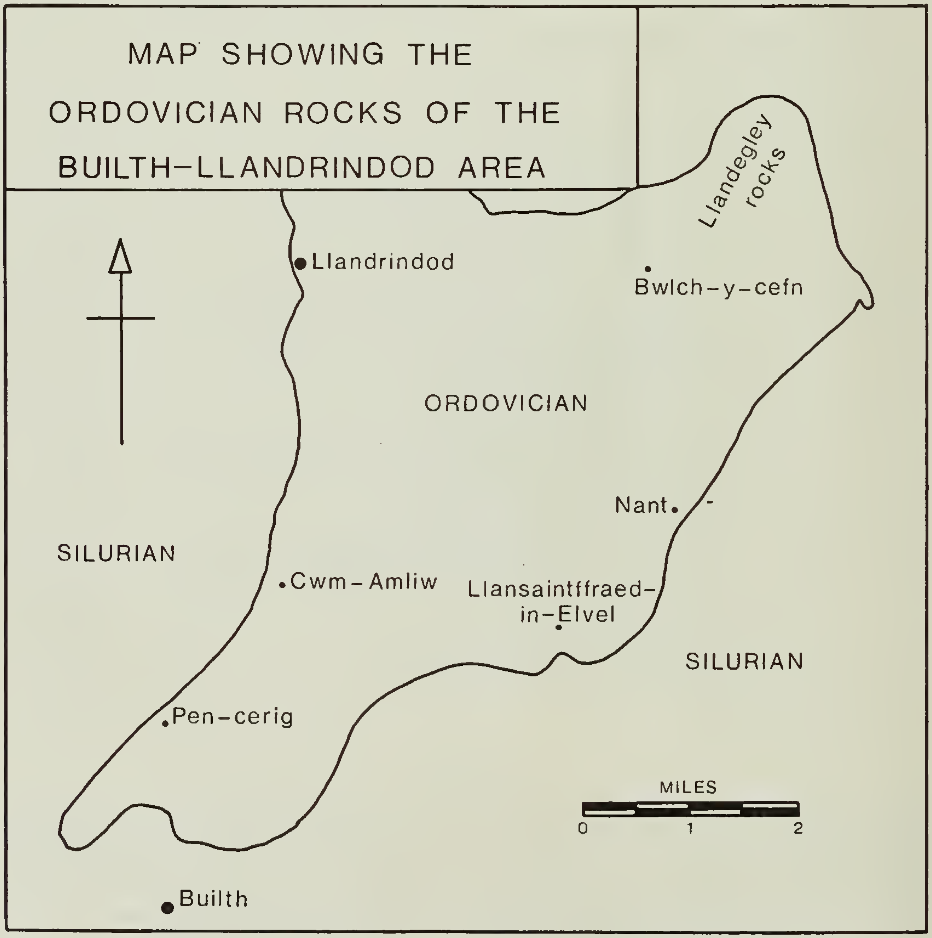

FIG. 1. Map showing the distribution of Ordovician rocks in the Builth-Llandrindod area. After Jones & Pugh 1941.

[1] Hereafter referred to as Llandrindod and Builth.

is situated approximately half-way between the well-known shelly Ordovician outcrops at Llandeilo (Williams 1948, 1953) and Shelve (Whittard 1931, 1940, 1940*a*, 1955–67).

Due to the presence of volcanic and intrusive rocks, the Ordovician inlier contrasts strongly with the gentler topography of the surrounding Silurian strata. Although

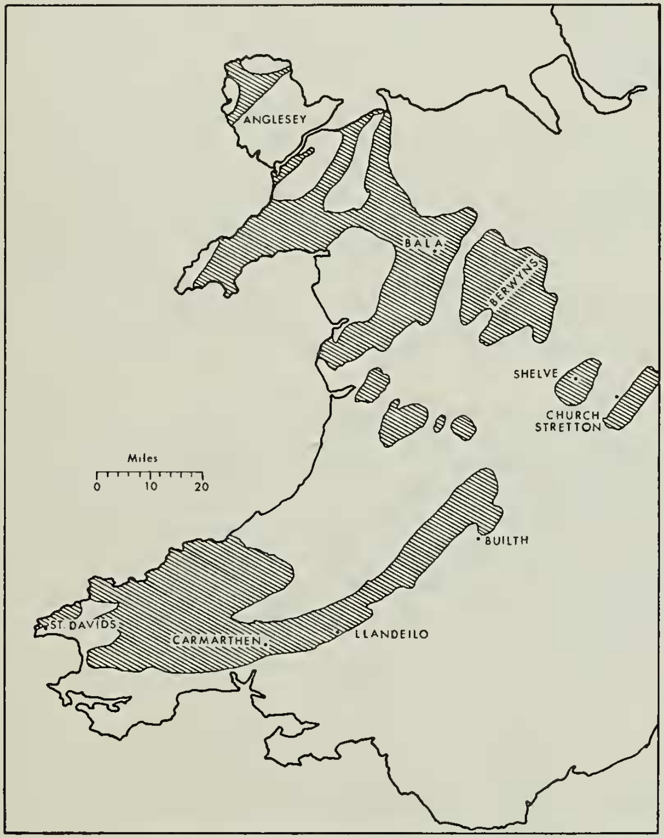

FIG. 2. Map showing the Ordovician outcrops of Wales and the Welsh Borderland together with the main localities yielding shelly faunas.

the intrusive and volcanic rocks of the inlier are well exposed, the sedimentary rocks are rarely seen in continuous section. In spite of numerous streams, surprisingly few are sufficiently free from superficial deposits to provide more than isolated outcrops, thus limiting the knowledge of the sedimentary succession which ranges from Lower Llanvirn (*murchisoni* Zone) to basal Caradoc (*gracilis* Zone).

The bulk of the material used for this study was collected by the author during the tenure, at the Queen's University of Belfast, of a research studentship awarded by the Natural Environment Research Council to whom I am grateful for financial

assistance. All type and figured material is deposited in the collections of the British Museum (Natural History), London, together with some further specimens. I am much indebted to Professor Alwyn Williams and Dr. A. D. Wright for their supervision and encouragement whilst the work was in progress and for critically reading much of the manuscript. My thanks are also given to Professor H. B. Whittington of the Sedgwick Museum, Cambridge, for much helpful advice and discussion in the later stages of the work. I am also indebted to Sir William Pugh and the late Professor O. T. Jones for generously supplying information concerning fossiliferous localities.

I thank Dr. D. A. Bassett and Mr. D. E. Evans, National Museum of Wales, Cardiff; Mr. A. G. Brighton and Dr. C. L. Forbes, Sedgwick Museum, Cambridge; Dr. D. L. Bruton, University of Oslo; Dr. F. M. Broadhurst, University of Manchester; Dr. W. T. Dean, British Museum (Nat. Hist.); Dr. V. Jaanusson, Naturhistoriska Riksmuseet, Stockholm; Mr. C. W. Newman, Radnorshire County Museum, Llandrindod Wells; Mr. W. J. Norton, Shropshire County Museum, Ludlow; Mr. H. P. Powell, University of Oxford; Dr. A. W. A. Rushton, Institute of Geological Sciences; Dr. I. Strachan, University of Birmingham; and Mr. J. T. Wattison, Stoke-on-Trent, for the loan of specimens in their care.

II. HISTORICAL REVIEW

The occurrence of trilobites in the Ordovician rocks of the Builth region has been known for a long time, being referred to by Murchison as long ago as 1833 (p. 476) when he recorded the occurrence of *Asaphus Buchii* in the dark trilobite flags of the Lower Silurian. A list provided subsequently by Murchison (1839 : 660, 662, 664) comprised the following five species from the region: *Agnostus pisiformis* Brongn.; *Asaphus Buchii* Brongn.; *Trinucleus*? *Asaphoides* (n.s.); *Trinucleus fimbriatus* (n.s.); *Trinucleus nudus* (n.s.).

In 1849 the faunal list was increased by M'Coy, who in describing some new fossils in the Cambridge University Collections, erected five species on specimens from the inlier, as follows: *Ampyx latus; Barrandia Cordai; Cryphaeus Sedgwickii, Ogygia radians; Trinucleus gibbifrons* var. Also in that year Salter recorded *Ogygia Portlockii* and *Asaphus Tyrannus* from Builth, and redescribed *Ogygia Buchii*, while *Ampyx nudus* was redescribed by Forbes.

In the period 1851–55 Sedgwick & M'Coy published their " Synopsis of the Classification of the British Palaeozoic rocks " in which the following eleven trilobite species were recorded from the Builth region: *Ampyx latus* (M'Coy); *Ampyx nudus* (Murch. Sp.); *Barrandia cordai* (M'Coy); *Diphlorhina triplicata* (Hawle and Corda)?; *Eccoptochile Sedgwickii* (M'Coy); *Isotelus* (*Basilicus*)? *laticostatus* (Green Sp.); *Isotelus* (*Basilicus*) *Powesii* (Murch.); *Ogygia buchii* (Brong. Sp.); *Ogygia radians* (M'Coy); *Tretaspis fimbriatus* (Murch. Sp.); *Trinucleus gibbifrons* (M'Coy).

Sedgwick & M'Coy's work was followed in 1864–83 by Salter's unfinished Monograph of the British Trilobites in which he described only eight trilobites from the Builth region, the following three being recorded for the first time: *Calymene duplicata* Murchison; *Ogygia angustissima* Salter; *Ogygia* (*Ptychopyge*) *corndensis* Murchison.

Ogygia portlockii, originally placed on the faunal list by Salter (1849), but omitted by Sedgwick & M'Coy (1851–55), was formally removed from the Builth faunal lists in this work.

Subsequent to 1866 no work on the trilobite fauna appeared until 1940 when Elles published her paper on the stratigraphy and faunal succession of the inlier. In this study Elles recorded 22 trilobites of which seven (denoted in the following list by an asterisk) were new: *Agnostus m'coyi* Salter; *Ampyx bisectus**; *Ampyx nudus* (Murchison); *Ampyx salteri* Hicks; *Barrandia cordai* (M'Coy); *Barrandia homfrayi* Hicks; *Barrandia* (*Homalopteon*) cf. *portlocki* Salter; *Barrandia* (*Homalopteon*) *radians* (M'Coy); *Calymene* (*Flexicalymene*) *aldonensis* (Reed); *Calymene* (*Platycalymene*) *duplicata* (Murchison); *Eccoptochile* (?) *sedgwicki* M'Coy; *Ogyginus corndensis* (Murchison); *Ogyginus corndensis* mut. *intermedius**; *Ogygiocaris buchi* (Brongniart); *Trinucleoides reticulatus**; *Trinucleus chamberlaini**; *Trinucleus fimbriatus* s.s. Murchison; *Trinucleus fimbriatus* mut. *primus**; *Trinucleus fimbriatus* mut. *ultimus**; *Trinucleus* cf. *foveolatus* Angelin; *Trinucleus* (*Cryptolithus*) *gibbosus**; *Trinucleus* (*Cryptolithus*) *lloydi* Salter.

Elles's paper is the most recent description of the Builth trilobites, although Whittard (1955–67) made some reference to the Builth fauna in his Monograph of the Shelve Trilobites.

The works cited above are concerned essentially with the trilobites and graptolites, the other faunal elements having received little attention. This is no doubt a reflection on the paucity of the other fossil groups, although brachiopods, bryozoa, conulariids, gastropods, lamellibranchs, ostracodes and sponges do occur in small numbers.

From the above lists it would appear that forms such as the cyclopygids, illaenids, marrolithinids and odontopleurids are absent from the Builth region. However, whilst the present study shows the Builth fauna to be less restricted than was formerly thought, it is still quite distinct from other Anglo-Welsh assemblages.

III. STRATIGRAPHICAL SUMMARY

The rocks of the inlier outcrop in a series of folds trending north-east to south-west. The plunge of the folds is variable and may be related to the numerous intrusions. The outcrops have been affected by faulting, particularly wrench faults, and this, together with the extraordinary burst of Llanvirn vulcanicity has led to complications in determining the succession and correlating from one part of the inlier to another. The stratigraphical succession as outlined by Elles (1940) and modified by Jones & Pugh (1941, 1948, 1949) has been used as the basis for the stratigraphical control of the fauna, although current field studies have necessitated some slight modifications. The dominant sedimentary types are mudstones and shales, which are interbedded with ashes and numerous doleritic intrusions. An exception to this is the Newmead Group with its more arenaceous deposits.

The thicknesses listed below are those given by Jones & Pugh (1948, 1949) and only include the thicknesses of the shale-mudstone sequence in the Lower Llanvirn, Llandeilo and Basal Caradoc. As indicated by these authors, if the thicknesses of the interbedded ashy beds are included then up to 10,000 feet of rocks are present in the southern part of the area, and slightly less in the northern part due to the thinning of the Upper Llanvirn sequence (see Text-fig. 3).

STRATIGRAPHICAL SUCCESSION

		Approximate thickness in feet
CARADOC	*Nemagraptus gracilis* shales with dolerite intrusions.	1,000
LLANDEILO	Shales and mudstones with occasional limestone and ash bands.	2,000
	UNCONFORMITY	
UPPER LLANVIRN	Upper *Didymograptus murchisoni* shales	0–400
	Cwm Amliw Ash	
	Rhyolitic Ash and ashy mudstones	150
	Newmead Group	
	Flinty mudstones	30
	Pyritiferous feldspar sands and boulder beds	160
	Grey feldspar sands and boulder beds	330
	UNCONFORMITY	
UPPER LLANVIRN	Builth Volcanic Group	
	Spilites, Keratophyres and Felsitic agglomerate	1,200
	Lower *Didymograptus murchisoni* shales	250
	Red agglomerate and Ash	500
	UNCONFORMITY	
	Llandrindod Volcanic Series	
	UNCONFORMITY	
LOWER LLANVIRN	*Didymograptus bifidus* shales with some ashy and more arenaceous bands	3,000

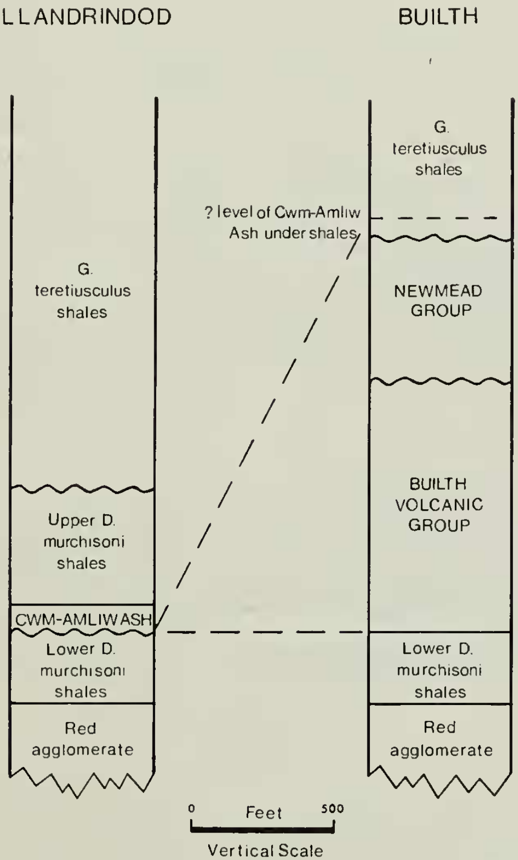

FIG. 3. Diagram showing the variation in the Llanvirn succession in the inlier. Modified after Jones & Pugh 1949.

Lower Llanvirn

This subseries consists of a thick sequence of about 3,000 feet, composed mainly of shales and mudstones, which are commonly micaceous, together with some more arenaceous bands. About 1,000 feet from the top of the subseries there is a widespread, almost continuous horizon of dolerite intrusions, with the beds above the dolerite becoming more ashy. The lower part of the succession, in general, is only sparingly fossiliferous, the fauna being restricted to a few trilobites and graptolites and occasional inarticulate brachiopods and small lamellibranchs. The beds near the top of the sequence yield a rich fauna of trilobites with some graptolites, brachiopods, sponges and larger lamellibranchs; these beds were assigned to the *Didymograptus speciosus* Subzone by Elles (1940).

Upper Llanvirn

This subseries may be considered as a shale-mudstone succession with a widespread development of volcanics and associated sediments in the middle of the sequence. Such a simple picture, however, is considerably modified because in the northern part of the inlier the great bulk of the volcanics were never developed; while to the south the upper part of the volcanics, together with the overlying shales, are overstepped by the *Glyptograptus teretiusculus* shales. Thus the Upper Llanvirn succession shows considerable variation within the inlier, the changes being summarized in Text-fig. 3. The fauna of the Upper Llanvirn consists basically of graptolites, which are exceedingly abundant at some localities. Trilobites are generally extremely rare, although some ogygiocaridinids appear towards the top of the succession. In the southern part of the inlier, the fauna of the Newmead Group reflects the different facies for it is made up almost exclusively of articulate brachiopods and sponge remains.

Llandeilo

This series is represented by about 2,000 feet of shales and mudstones with an occasional thin limestone and calcareous ash band. Numerous small doleritic intrusions are present, being most likely confined to two horizons, one in the lower and the other in the upper part of the succession (Jones & Pugh 1946). As in the higher Lower Llanvirn, trilobites are more common than graptolites; inarticulate brachiopods, lamellibranchs, ostracodes and sponges also occur sporadically throughout the succession but only as a minor element of the fauna.

Basal Caradoc

Where exposed this succession almost invariably consists of dark indurated shales and mudstones, near, or in contact with the numerous dolerite intrusions. Jones & Pugh (1948) estimated the thickness of the *N. gracilis* shales to be about 1,000 feet although the upper part is poorly exposed. While the trilobites continue to form a prominent part of the fauna, the graptolites are also very abundant at several horizons. Inarticulate brachiopods, gastropods, and less commonly articulate brachiopods, nautiloids and sponges are also present.

IV. THE USE OF BIOMETRICAL TECHNIQUES

Since the early pioneer work on the application of biometrical techniques in palaeontological studies by such workers as Burma (1948), Kermack & Haldane (1950), Kermack (1954) and Imbrie (1956), the use of statistical procedures in the study of fossil populations is being slowly accepted in many branches of palaeontology. There has however been a general reluctance, with a few notable exceptions, on the part of trilobite workers to adopt these techniques. This may be due, as Williams (1962 : 70) pointed out, to a general belief among many palaeontologists that the use of statistical techniques is unnecessary in assessing the degree of morphological similarity, as that can be done effectively by the experienced systematist without recourse to statistics. While this may be true in certain cases, depending on the individual worker, no verbal description can communicate the amount of variation in characters so precisely as a statistic or series of statistics. Another reason for the non adoption of biometric techniques in trilobite studies may be the fragmentary nature of so much trilobite material; this, however, cannot be used as a valid argument against the use of statistical methods whenever the available material permits.

In considering continuously variable parameters, such as length and width, bivariate analyses have been generally found, by workers on differing phyla, to be satisfactory. This form of treatment was fully described by Kermack & Haldane (1950) and Kermack (1954). Apart from its comparative simplicity, this form of analysis has the advantage over multivariate analyses of indicating precisely which characters are similar and which show differences. This identification of changes affecting single characters is important in dealing with temporal as well as spatial variations because it provides a means of unravelling evolutionary trends. Bivariate analysis is also a well-tested method for taxonomic discrimination, although it is more cumbersome than the multivariate techniques which give an overall idea of similarity or dissimilarity. By means of various biometric techniques adopted here, it has been possible: firstly to supplement the specific diagnoses with measures of variation affecting many characters; secondly to investigate growth patterns typical of fossil trilobite populations and the occurrence of holaspid instars.

Before the normal biometric techniques can be applied to the Trilobita however, the possible effects of the discontinuous mode of skeletal growth found in the arthropods must be considered. It is clear, since increase in size of a typical arthropod can only take place between the shedding of one exoskeleton and the hardening of the next, that the theoretical growth curve relating any two size parameters will never be realized in the life-history of any single individual. Instead, both parameters, based on exoskeletal dimensions, will increase in size by a series of jumps, although the points thus arrived at will all be on the theoretical curve.

Although moulting of many arthropods, including some trilobites, tends to occur at each doubling of weight (Przibram 1931; Hunt 1964, 1967), the natural variation within a sample, coupled with variations in initial post-larval weight are in some instances sufficient to obscure any recurrent modality in the sizes at which moulting occurs. In a large population of such a species, moulting will thus take place randomly at any size, and the measurements of exoskeletal parameters should fall on a continuous curve. In those cases where a recurrent modality in moult size is apparent, the measurements obtained of exoskeletal parameters in any sample will still lie along the theoretical growth curve, and will differ from the former case only in that there will be intervals along the curve in which no measurements occur.

It is thus seen that the mode of growth of trilobites presents no reasons against using the bivariate techniques proposed by Kermack & Haldane (1950) and Kermack (1954), although there may be some bias towards the smaller individuals due to the presence of exuviae in a sample.

Owing to the periodic renewal of the entire exoskeleton, growth lines are absent and no indication of the former shape of an individual can be obtained. Thus damaged specimens cannot be utilized to give measurements for an individual when at an earlier growth stage as is possible, for instance, with brachiopods. This fact can often seriously reduce the amount of data obtainable from a sample. The lack of growth lines also means that in a water-sorted sample the data obtainable are strictly limited to the size of the individuals present and no data can be deduced for individuals smaller than those represented in the sample. Although the mechanics of hydrodynamical sorting are still not adequately understood, it is safe to assume that the variability of characters in a water-sorted sample will be less than in a natural population. Williams (1962 : 72) considered that the effect of water sorting on systematic studies of brachiopods could be disastrous were it not for the preservation of growth lines which record the development of the exoskeletons of most individuals. Whilst this does not rule out the use of biometric techniques in trilobite studies, it does, in certain cases restrict knowledge of the growth and development to a relatively small size range. Great caution must therefore be exercised in distinguishing between forms which are inferred from samples to be of different absolute size.

Thus it is seen that neither the discontinuous nature of the skeletal growth nor the absence of growth lines on the exoskeleton precludes the use of statistical treatments already in use for organisms like echinoderms and brachiopods which are subject to continuous skeletal growth. The lack of growth lines does however mean that more assiduous collecting is necessary to obtain a sufficient sample size, and even in moderately large samples, knowledge may be restricted to a limited size range. This need for protracted collecting is still not a valid reason against using biometrical techniques whenever possible. In the present study the various techniques and notation have been used as originally outlined by Kermack & Haldane (1950) and Kermack (1954) and subsequently adopted and enlarged on by Williams (1962).

Unless some care is taken in collecting, faunal samples from any particular outcrop or region may show a considerable degree of " collector's bias ". This has been discussed by Kermack (1954) and Simpson, Roe & Lewontin (1960) and in the present study an effort was made to reduce this to a minimum. In only two localities were fossil remains sufficiently abundant to make bulk sampling possible. These were the cliff section in the Howey Brook where the so-called " *Trinucleus* " band consists of little other than trilobite remains and in the upper reaches of the Camnant Brook where a rotten stone band crops out which is largely fossil debris. Where the dispersed distribution of trilobites rendered the collection of bulk samples impracticable every trilobite fragment was retained to avoid the necessity of making field selections of the " best " specimens. At certain localities however, like the middle quarry at Llanfawr where trilobites are very common, some selection inevitably occurred. It is thus felt that the samples obtained are reasonably free from bias.

The single orientation method of measurement proposed by Shaw (1957) has been adopted throughout. In those measurements involving distances between, or to, furrows, the measurements have been taken from the deepest (dorsoventrally) point in the furrow. A micrometer ocular was used for all measurements under 2 cm. Larger measurements were made using vernier calipers.

Although the notation proposed by Shaw (1957) and adopted by Hunt (1967) for various measurements is useful, particularly in standardizing measurements of various species, it is rather unwieldy if applied too rigidly. Consequently it has been decided to define the measurements made for each family independently, although standard "code letters" have been retained throughout. Thus "A" always refers to measurements of cephalic length; "K" to glabellar width; "Z" to pygidial length measurements.

The selection of parameters for measurement must be to some extent subjective. This introduces a contradiction, for the aim of using statistical techniques is to be as objective as possible (see Olson & Miller 1951 : 218). In respect to trilobites, selection of the most suitable measurements is not always clear due to a general lack of knowledge of growth mechanisms. Moreover selection is often strongly influenced by the amount, and state of preservation, of the material available. All the data given in the present study are taken from internal moulds and have been selected, as far as possible, to define the major elements of the exoskeleton. However it must be stressed that this selection is subjective and it is for future research to judge which are the most important and useful parameters, both taxonomically and for our understanding of trilobite growth and evolution. By limiting measurements to those which may be termed "basic" characters it is hoped that growth patterns within the trilobites may be found, although the limited coverage of the present work does not reveal any such patterns.

V. TERMINOLOGY

The morphological terms proposed by Harrington, Moore & Stubblefield *in* Moore (1959) have been adopted throughout with the exception of a few terms either in use or introduced since that date, together with certain new terms here introduced. Such terms applied only to particular families or other taxa will be listed in the appropriate part of this series.

Intra-axial furrow—This term is proposed for the furrow between the middle and lateral lobe of the thoracic axial ring of agnostids.

Occiput—This term introduced by Stäuble (1953 : 87) and adopted by Whittington (1959 : 441) is here accepted.

Pleural ridge—This term is used for any ridge running in a general transverse direction across the thoracic pleura.

Terminal area (of pygidium)—This term is introduced in species having a ribbed pleural field for that part of the pleural field posterior to the last furrow.

VI. DEFINITION OF MEASUREMENTS

Measurements taken on agnostids (see Text-fig. 4)

A	maximum cephalic length—measured in the sagittal line.
A_1	intraborder cephalic length—measured in the sagittal line between the posterior margin of the cephalon and the anterior border furrow.
B	glabellar length—measured in the sagittal line from the posterior of the glabella to the preglabellar furrow.
B_1	the distance from the posterior of the glabella to the intersection of the axial furrow and the transglabellar furrow, as projected onto the sagittal line.
B_2	the distance from the posterior of the glabella to the transglabellar furrow as measured in the sagittal line.

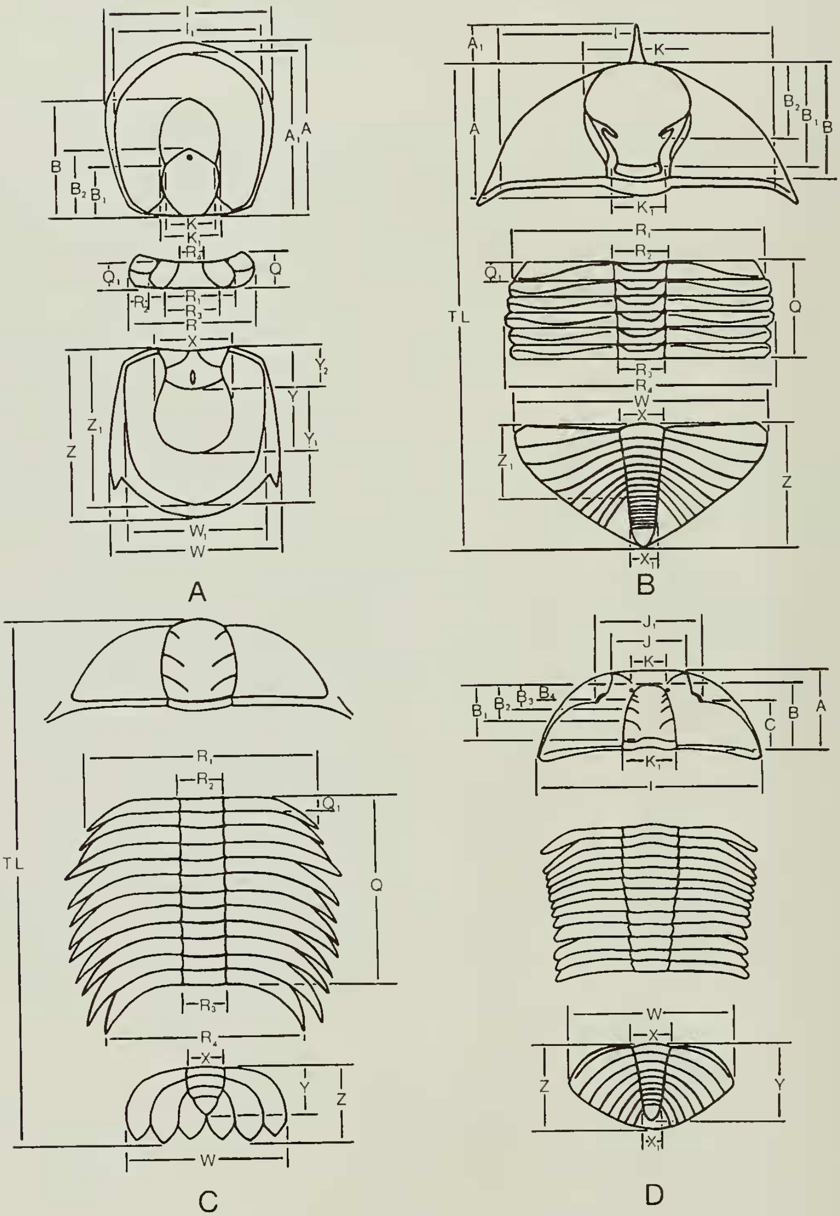

FIG. 4. Diagram showing the measurements taken on agnostids, raphiophorids, *Placoparina* and calymenids.

I maximum cephalic width—measured in a transverse direction.

I_1 maximum intraborder cephalic width—measured in a transverse direction between the lateral border furrows.

K transverse furrow glabellar width—measured in a transverse direction between the axial furrows at the intersections of the transglabellar furrow and the axial furrows.

K_1 maximum glabellar width—measured in a transverse direction between the axial furrows.

Q anterior thoracic segment length—measured between the most anterior and posterior portions of the segment as projected onto an exsagittal line.

Q_1 axial length of anterior thoracic segment—measured in the sagittal line.

R maximum anterior thoracic segment width—measured in a transverse direction.

R_1 maximum width of thoracic axis—measured in a transverse direction between the lateral extremities of the axial ring.

R_2 pleural width of anterior thoracic segment—measured between the lateral extremity of the pleura and the posterolateral extremity of the axis as projected onto a transverse line.

R_3 posterior width of median axial lobe—measured in a transverse direction along the posterior of the segment between the intra-axial furrows.

R_4 anterior width of median axial lobe—measured in a transverse direction along the anterior of the segment between the intra-axial furrows.

W maximum pygidial width—measured in a transverse direction.

W_1 maximum intraborder pygidial width—measured in a transverse direction between the lateral border furrows.

X maximum axial width—measured in a transverse direction.

Y axial length—measured in the sagittal line from the anterior margin to the postaxial furrow.

Y_1 the distance from the transverse axial furrow to the posterior border furrow, as measured in the sagittal line.

Y_2 the distance between the anterior margin of the pygidium and the transverse axial furrow as measured in the sagittal line.

Z pygidial length—measured in the sagittal line between the anterior and posterior margins of the pygidium.

Z_1 maximum intraborder pygidial length—measured in the sagittal line between the anterior margin of the pygidium and the posterior border furrow.

Measurements taken on raphiophorids (see Text-fig. 4)

A cephalic length—measured in the sagittal line from the posterior margin to the anterior of the glabella, excluding the frontal glabellar spine.

A_1 length of frontal glabellar spine—measured in the sagittal line.

B glabellar length—measured in the sagittal line between the occipital furrow and the anterior of the glabella.

B_1 the distance between the " posterior lateral glabellar furrows " and the anterior of the glabella as measured in the sagittal line.

B_2 the distance between the posterior extremity of the " anterior lateral glabellar furrows " and the anterior of the glabella, as projected onto the sagittal line.

I cephalic width—measured in a transverse direction between the points of deflection of the posterior margin.

K anterior glabellar width—measured in a transverse direction between the axial furrows at the maximum width of the glabella.

K_1 posterior glabellar width—measured in a transverse direction between the axial furrows at the maximum width of the " basal glabellar lobe ".

Q thoracic length—measured in an exsagittal line between the anterior margin of the anterior segment and the posterior margin of the posterior segment.

Q_1 length of anterior thoracic segment—measured in an exsagittal line between the anterior and posterior margins of the anterior thoracic segment.

R_1 anterior thoracic width—measured in a transverse direction between the lateral extremities of the posterior margin of the anterior thoracic segment.

R_2 anterior thoracic axial width—measured in a transverse direction between the axial furrows along the anterior of the anterior axial ring.

R_3 posterior thoracic axial width—measured in a transverse direction between the axial furrows along the posterior of the posterior axial ring.

R_4 midthoracic width—measured in a transverse direction between the lateral extremities of the posterior margin of the third thoracic segment.

W maximum pygidial width—measured in a transverse direction.

X anterior pygidial axial width—measured in a transverse direction between the axial furrows along the anterior margin.

X_1 posterior pygidial axial width—measured in a transverse direction between the axial furrows at the posterior of the parallel-sided portion of the axis.

Z pygidial length—measured in the sagittal line between the anterior margin and the posterior of the axis.

Z_1 the distance between the anterior margin and the join of the hindmost furrow on the pleural field with the axial furrows, as measured in an exsagittal line.

T.L. total length—measured in the sagittal line between the anterior of the glabella (excluding the frontal glabellar spine) and the posterior of the pygidial axis.

Measurements taken on *Placoparina* (see Text-fig. 4)

Q thoracic length—measured in an exsagittal line between the anterior margin of the anterior thoracic segment and the posterior margin of the posterior thoracic segment.

Q_1 anterior thoracic segment length—measured in an exsagittal line between the anterior and posterior margins of the anterior thoracic segment.

R_1 anterior thoracic width—measured in a transverse direction between the distal extremities of the anterior thoracic segment.

R_2 anterior thoracic axial width—measured in a transverse direction along the posterior of the anterior thoracic axial ring between the axial furrows.

R_3 posterior thoracic axial width—measured in a transverse direction along the posterior of the posterior thoracic axial ring between the axial furrows.

R_4 posterior thoracic width—measured in a transverse direction between the distal extremities of the posterior thoracic segment.

W maximum pygidial width—measured in a transverse direction.

X anterior pygidial axial width—measured in a transverse direction along the anterior margin between the axial furrows.

Y pygidial axial length—measured in the sagittal line between the articulating half ring furrow and the posterior of the axis.

Z pygidial length—measured between the articulating half ring furrow and the posterior tip of the second pair of pleural terminations, as projected onto the sagittal line.

T.L. total length—measured between the anterior margin of the glabella and the posterior tip of the second pair of pleural terminations, as projected onto the sagittal line.

Measurements taken on calymenids (see Text-fig. 4)

A cephalic length—measured in the sagittal line between the anterior and posterior margins of the cephalon.

B cephalic axial length—measured in the sagittal line between the posterior margin of the cephalon and the preglabellar furrow.

B_1 glabellar length—measured in the sagittal line between the occipital furrow and the preglabellar furrow.

B_2 the distance between the preglabellar furrow and the intersection of the *1*p lateral glabellar furrows and the axial furrows, as projected onto the sagittal line.
B_3 the distance between the preglabellar furrow and the intersection of the *2*p lateral glabellar furrows and the axial furrows, as projected onto the sagittal line.
B_4 the distance between the preglabellar furrow and the intersection of the *3*p lateral glabellar furrows and the axial furrows, as projected onto the sagittal line.
C postpalpebral length—measured between the posterior of the palpebral lobe and the posterior margin of the cephalon, as projected onto the sagittal line.
I maximum cephalic width—measured in a transverse direction.
J anterior cranidial width—measured in a transverse direction between the anterior extremities of the cranidium.
J_1 mid cranidial width—measured in a transverse direction between the posterior of the palpebral lobes.
K anterior glabellar width—measured in a transverse direction between the anterior fossulae.
K_1 posterior glabellar width—measured in a transverse direction between the axial furrows along the posterior cephalic margin.
W maximum pygidial width—measured in a transverse direction.
X anterior pygidial axial width—measured in a transverse direction between the axial furrows along the anterior margin.
X_1 posterior pygidial axial width—measured in a transverse direction between the axial furrows at the posterior of the axis.
Y pygidial axial length—measured in the sagittal line between the anterior pygidial margin and the posterior of the axis.
Z pygidial length—measured in the sagittal line.

VII. SYSTEMATIC DESCRIPTIONS

Family **AGNOSTIDAE** M'Coy 1849

Genus ***GERAGNOSTUS*** Howell 1935

1939 *Geragnostella* Kobayashi.

Diagnosis. Agnostids with transglabellar furrow and axial furrows variously developed; no longitudinal preglabellar furrow. Pygidial axis generally slightly more than half pygidial length; trilobed; short posterolateral spines present. Dorsal surface smooth.

Type Species. *Geragnostus sidenbladhi* (Linnarsson 1869).

Distribution. The genus ranges from the Tremadoc to Llandeilo Series and is widely distributed throughout Europe, North and South America and China.

Discussion. Considerable difficulties are encountered in distinguishing between *Geragnostus* and *Trinodus* M'Coy 1846 and both Ross (1958 : 563–564; 1967 : 8–9) and Whittington (1963 : 28; 1968) have discussed this question. Until recently it seemed possible that within the genus there were two groups, of possible subgeneric or even generic rank, one characterized by a well-developed transglabellar furrow and the other by the poor development or complete absence of such a furrow. Ross (1967 : 8–9) has followed Whittard (1966 : 265) in stressing the importance of this furrow, advocating that those forms with no transglabellar furrow be referred to

Trinodus, and those with, to *Geragnostus*. This subdivision would appear to be straightforward but for Dean's (1966 : 275–276) discovery that *Geragnostus occitanus* Howell 1935 shows considerable variation in the degree of development of the transglabellar furrow and axial furrows which are clearly present in some specimens any almost completely absent in others. Thus it would now seem unwise to consider and possible generic separation based on the development of these furrows. Dean (1966 : 274) has suggested that further research may show *Geragnostus* to be a junior synonym of *Trinodus*; however, until new material of the type species of *Trinodus*, *T. agnostiformis* M'Coy is described, some confusion between these genera will continue.

Having shown that the axial furrows may not always be developed around the posterior of the pygidial axis in *Geragnostus*, Dean (1966 : 273) placed *Geragnostella* Kobayashi 1939 in synonymy with *Geragnostus* on the grounds that the pygidial axis of *Geragnostella* could no longer be held as different from that of *Geragnostus*.

Although many of the species of *Geragnostus* are of limited geographical range, the wide occurrence of the genus makes it of particular use in the study of faunal provinces.

Geragnostus mccoyii (Salter *in* Murchison)

(Pl. 1, figs. 1–12)

1839 *Agnostus pisiformis* (Wahlenburg); Murchison : 650, 664, 704, pl. 25, figs. 6a, 6b.
1851 *Diplorhina triplicata* M'Coy *in* Sedgwick & M'Coy : 142, pl. 1E, fig. 11.
1854 *Agnostus McCoyii* Salter *in* Murchison : pl. 3, fig. 8.
1859 *Agnostus maccoyii* Salter *in* Murchison : pl. 3, figs. 7, 8, Foss. 10, fig. 5.
1939 *Geragnostus* (*Corrugatagnostus*) *maccoyi* (Murchison); Kobayashi : 173.
1955 *Geragnostus maccoyi* (Murchison); Whittard : 8, pl. 1, figs. 5, 6.
1966 *Geragnostus maccoyii* (Murchison); Whittard : 265–266, pl. 46, fig. 2. Includes full synonomy.

Diagnosis. *Geragnostus* with glabella approximately bisected by chevron-shaped transglabellar furrow, with small median glabellar node immediately to posterior; lateral occipital lobes present. Pygidial axis with anterior lateral lobes and two segments, posterior one being about two-thirds of axial length; median node present on anterior segment; axial furrows sinuous with axis constricted opposite transverse furrow.

Lectotype. GSM. 8710 (Stokes Coll.). (Pl. 1, figs. 1, 2.) Internal mould of cephalon. Figured by Murchison 1839, pl. 25, fig. 6b as *Agnostus pisiformis*. Designated and refigured by Whittard 1955 : 8, pl. 1, fig. 5.

Dimensions.

A	A_1	B	B_1	B_2	I	I_1	K	K_1
3·1	2·8	2·1	1·1	0·9	3·4	3·0	1·2	1·1

All measurements in mm. For explanation of symbols see Text-fig. 4.

Type locality and horizon. The precise locality for the lectotype is not certain, but it is most likely the small quarry at the south-western end of Pen-cerig Lake, in beds of uppermost Llandeilo age.

Other figured material. It. 2670 (Pl. 1, figs. 4, 8); It. 2671 (Pl. 1, fig. 3); It. 2673 (Pl. 1, fig. 12); It. 2675 (Pl. 1, fig. 9); It. 2677 (Pl. 1, fig. 10); It. 2680 (Pl. 1, fig. 11); GSM. 8709 (Pl. 1, figs. 5, 6); Wattison Coll. H1 (Pl. 1, fig. 7).

Distribution. The species is virtually confined to the Builth-Llandrindod inlier where it occurs in beds of the Llandeilo and basal Caradoc Series (*teretiusculus* and *gracilis* Zones). A single specimen, however, has also been recorded from the Meadowtown Beds (Llandeilo) of the Shelve district (Whittard 1966 : 266).

Description. The roundedly subquadrate cephalon tends to be slightly wider than long. The subcylindrical glabella, rounded in front and smooth, is moderately convex, occupies, in general, a little over two-thirds of the cephalic length and is defined by deep axial furrows. A single conspicuous transglabellar furrow, present at about the mid-glabellar length, is markedly convex forwards, giving a concavo-convex outline to the anterior glabellar lobe; the anterior lobe being in general fractionally wider than the posterior lobe. On external moulds a small median glabellar node is present immediately behind the transglabellar furrow (Pl. 1, fig. 10); there is also a suggestion of its development on many well-preserved internal moulds (Pl. 1, figs. 1, 11). Prominent triangular lateral occipital lobes are developed. The genae are smooth, gently and evenly convex, commonly narrowing slightly in front of the glabella. The border is separated by a deep, moderately wide border furrow with moderately sloping sides, becoming steeper and narrower at the postero-lateral corners and along the posterior edge of the genal regions (Pl. 1, fig. 11). Although the posterolateral corners are rarely well preserved, the small spines described by earlier authors (e.g. Salter 1864*a*) are not present, although there may be a slight swelling of the border.

The thorax consists of two segments, the anterior one being the larger (Pl. 1, figs. 5, 7). The axis of the anterior segment is broad and divided into a median trapezoidal lobe and a pair of oval lateral lobes with major axes directed inwards and forwards at about 45°; the pleurae are divided by pleural furrows into nearly equal bands. The posterior segment is similar, differing chiefly in that the major axes of the oval lateral lobes lie in a transverse direction. The pleurae of both segments are curved forwards.

The subquadrate pygidium, like the cephalon, is typically slightly wider than long. The axis, rounded posteriorly, is slightly over one-half of the pygidial length and is slightly constricted just to the anterior of the transverse furrow. This furrow is well developed, gently concave anteriorly, and occurs at about one-third the length from the anterior of the axis. Immediately anterior of this is an elongated median node. At the anterolateral corners of the axis are a pair of prominent lobes. The pleural lobes are smooth, more or less constant in width and convexity and are limited by a deep border furrow. A convex border is present laterally and posteriorly, becoming steeply upturned along the anterior margin of the pleural lobes. Small spines are present at the posterolateral corners (Pl. 1, fig. 4).

Ontogeny. Small holaspid individuals appear to differ little from the largest. Specimen It. 2673 (Pl. 1, fig. 12) however most likely represents a meraspid degree one. This specimen is similar to the one figured by Whittington (1965 : pl. 2, figs.

14, 18) as a meraspid degree one of *Geragnostus fabius* (Billings 1865) in that it shows the pleural region of what is to become the pleura of the second thoracic segment. Unfortunately the axial portion of the embryo thoracic segment is not preserved in the Builth specimen. Unlike Whittington's specimen, the remainder of the axis of the transitory pygidium is divided into two nearly equal lobes, the posterior one being slightly larger. Thus the axis is very similar to the glabella of a small holaspid and the possibility that this specimen represents a very small cephalon with a particularly wide posterior border must remain. The dimensions of this individual are; length 1·14 mm; width 1·32 mm. Four other small pygidia varying in length from 1·4–1·9 mm. all appear to be small holaspids.

Biometrical data. Sample populations from the Llandeilian rocks exposed in the stream section east of Bach-y-graig 40 yards east of the point where the footpath enters the wood at the western end of the section and the small quarry at the south-western end of Pencerig Lake were tested for differences in the growth ratios (a or α) and initial growth shape (b or β); no statistically significant differences were found. The following Tables have been compiled by using the combined samples.

Table 1

x : y	$\bar{x}$	var. x	y	var. y	r	r_e	α	var. α	a	var. a	n
$A_1 : I_1$.	3·14	0·44	3·06	0·45	0·93	0·94	1·04	0·0037	1·02	0·0047	33
$A_1 : B$.	3·15	0·55	2·27	0·31	0·99	0·99	1·03	0·0006	0·74	0·0001	43
$B : B_2$.	2·26	0·27	1·24	0·09	0·97	0·98	1·05	0·0004	0·58	0·0012	47
Z : W .	2·85	0·68	2·86	0·78	0·94	0·94	1·07	0·0050	1·07	0·0052	28
Y : Z .	1·91	0·30	2·92	0·62	0·99	0·99	0·94	0·0006	—	—	40
$Y_2 : Y$.	0·73	0·05	1·86	0·30	0·81	0·81	0·94	0·0080	2·41	0·0544	39

Bivariate statistics for the cephalon and pygidium of *G. mccoyii* (Salter *in* Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

Table 2

Q	Q_1	R	R_1	R_2	R_3	R_4
1·0	0·6	3·1	2·0	0·6	1·1	0·4
0·9	0·5	—	—	—	—	—
—	0·6	—	—	—	—	—

Thoracic measurements of three specimens of *G. mccoyii* (Salter *in* Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

In view of the use of various ratios in discriminating certain species within this genus the means and variance for various ratios along with their observed ranges are given in Table 3.

The relatively large variation in the ratio $Y_2 : Y$ may be due to the fact that its variance is dependent on the variance of both Z_1 and Y_1 ($Y_2 = Z_1 - Y_1$).

An attempt has been made to see whether the shape of the transglabellar furrow altered with size. As expected the value of $B_2 - B_1$ increases with the value of B

TABLE 3

Ratio	Mean	var.	Observed range	n
$B_2 : B$	0·55	0·001	0·47–0·60	47
$B : A$	0·66	0·001	0·55–0·72	31
$Y_2 : Y$	0·39	0·005	0·27–0·56	39
$Y : Z$	0·59	0·002	0·47–0·69	34

Statistical data for various ratios for *G. mccoyii* (Salter *in* Murchison). For explanation of symbols see Text-fig. 4.

(see Table 4), but the ratio $B_2 - B_1 : B$ does not show a similar increase (see Table 5). Thus it is seen that the amount of forward convexity increases more or less proportionately with increase in glabellar length.

TABLE 4

B in mm.		1·5–1·9	2·0–2·4	2·5–2·9	3·0–3·5
$B_2 - B_1$ in	0·1	5	—	—	—
mm.	0·2	3	10	3	—
	0·3	—	4	6	4

Data showing the increase in the value of $B_2–B_1$ with increase in B for *G. mccoyii* (Salter *in* Murchison). For explanation of symbols see Text-fig. 4.

TABLE 5

B in mm.	1·5–1·9	2·0–2·4	2·5–2·9	3·0–3·5
Range in value of	0·056	0·083	0·074	0·097
$B_2 - B_1 : B$	to	to	to	to
	0·13	0·15	0·12	0·10

Ranges in the value of the ratio $B_2–B_1 : B$ for corresponding values of B for *G. mccoyii* (Salter *in* Murchison). For explanation of symbols see Text-fig. 4.

DISCUSSION. In the past there has been some confusion over the spelling of *mccoyii*, but the original spelling of Salter *in* Murchison 1854 should be retained.

As was pointed out by Whittard (1966 : 266) the radial ornament on the genae described by Salter (1864*a* : 6, pl. 1) is simply due to cracking of the exoskeleton and Kobayashi (1939 : 173) was mistaken in placing the species in *Corrugatagnostus* Kobayashi 1939.

G. mccoyii may be distinguished from many other species of the genus, including *G. sidenbladhi*, by its well-developed axial and transglabellar furrows. Of those species with a transglabellar furrow well developed, it resembles most closely *Geragnostus hirundo* (Hicks 1875) from the " Middle Arenig " of Whitesand Bay. *G. mccoyii* differs however in the squarer cephalic outline and the greater anterior convexity of the transglabellar furrow; the pygidium of *G. mccoyii* is distinguished by the transverse furrow occurring at about one-third, instead of one-half, the distance along the pygidium as measured from the anterior margin. *G. caducus* (Barrande 1872) from the Dd_1 beds at Sancta Benigna is easily distinguished by the development of a second transverse glabellar furrow and its more prominent median glabellar node. Tjernvik (1956 : 188 ff.) erected four new species of *Geragnostus*: *G. crassus*, *G. lepidus*, *G. wimani* and *G. explanatus*. *G. mccoyii* differs from all these in that the transglabellar furrow is more strongly developed. *G. mccoyii* is distinguished from *G. occitanus* Howell 1935, and *G. mediterraneus* Howell 1935, by its better and more constantly developed axial and transglabellar furrows and also in the shorter axis of the pygidium.

The internal and external moulds are very similar and apart from the lateral pygidial borders, differ only in that the furrows are somewhat deeper and broader on the internal moulds than on the external ones. This is in general agreement with Whittington's findings on *Geragnostus clusus* Whittington (Whittington 1963 : 30) and also with Dean's work on *G. occitanus* Howell 1935 (Dean 1966 : 274–276). However variation in the development of the transglabellar and axial furrows as found by Dean in *G. occitanus* is unknown in *G. mccoyii*. It is noted that a furrow is present on some internal moulds on the outer portion of the lateral pygidial borders, anterior to the posterolateral spines and subparallel to the lateral margin (Pl. 1, fig. 4). No trace of such a furrow is to be found on external moulds (Pl. 1, fig. 8) and it is believed that the furrow may indicate the presence on the ventral side of the doublure of a structure for interlocking the cephalon and pygidium on enrollment. Similar though not identical structures are known in *Trinodus elspethi* (Raymond 1925) (Hunt 1964, pl. 2, fig. 9), and in *Baltagnostus eurypyx* Robison 1964 and *Peronopsis interstricta* (White 1874) (Robison 1964, pl. 80, fig. 14; pl. 82, fig. 14).

The thoracic segments are of the usual agnostid pattern. Their general form supports Whittington's conclusion that the oval lateral lobes are axial and not pleural structures, although they do differ in certain respects from those of *G. clusus* as described by Whittington (1963 : 29, 32, text-fig. 3). The most striking difference is in the size of the median and lateral axial lobes of the anterior segment. In *G. clusus* they occupy only the posterior part of the segment, whereas in *G. mccoyii* they occupy the whole of the axis; the anterior margin of the segment, too, is concave forwards, whereas in *G. clusus* it is more or less straight; and no median notch is seen in *G. mccoyii*. The posterior segments are in general very similar in the two species, although the form of the articulating half ring is not known in *G. mccoyii*.

Out of the eight complete or nearly complete specimens known, three show rotation of the cephalon and thorax relative to the pygidium (Pl. 1, fig. 3); the other five, although they may be slightly disarticulated, show no rotation of the various elements relative to one another. It is tentatively suggested that the specimens showing rotation may be the exoskeletons of moults and those showing no rotation, individuals that died.

Apart from its occurrences in the Builth area the species has in the past (Hicks 1875 : 180) been recorded from South Wales, but the poor preservation of these specimens makes his identifications questionable. The species has also been recorded from the Upper Lingula Flags at Malvern, although as was pointed out by Groom (1902 : 103) these specimens are almost certainly *Agnostus trisectus*.

Genus *SPHAERAGNOSTUS* Howell & Resser 1936

DIAGNOSIS. Cephalon smooth, convex, without furrows. Pygidium somewhat smaller than cephalon, with subcircular axis occupying over half the area of the exoskeleton.

TYPE SPECIES. *Sphaeragnostus similaris* (Barrande 1872).

DISTRIBUTION. Known from the Upper Tremadoc of Kendykyas (USSR), Llandeilo of Bohemia and Britain, Middle Ashgill of Poland, Quebec and Sweden and also possibly from the Lower Ashgill of Ireland.

DISCUSSION. Despite its wide geographical distribution the genus is extremely rare, being known from only a few specimens of each of the species. Its occurrence in the Builth district is of interest as it is the first record of the genus from the Llandeilo Series of the British Isles.

Sphaeragnostus sp.

(Pl. 1, figs. 13–15)

FIGURED MATERIAL. It. 2681 (Pl. 1, figs. 13, 15). Internal mould of pygidium. It. 2682 (Pl. 1, fig. 14). Internal mould of pygidium.

DIMENSIONS.

	W	X	Y	Z
It. 2681	c. 2·8	1·6	1·6	2·7
It. 2682	c. 3·1	1·8	1·7	2·8

All measurements in mm. For explanation of symbols see Text-fig. 4.

LOCALITIES AND HORIZON. The species is known from the old quarry 350 yards west of Maesgwynne (It. 2682); the stream section 15 yards south-west of this quarry; and the left bank of the stream section in the Dulas Brook 150 yards south-west of this quarry and 60 yards north of spot height 727 (It. 2681). All these occurrences are in the Llandeilo Series.

DESCRIPTION. The cephalon and thorax are unknown.

The subcircular pygidium is truncated anteriorly and slightly elongated sagittally. The subcircular axis, occupying about three-fifths of the pygidial length, is moderately convex, and possesses a median node slightly anterior of its centre. The axial furrows are deep and of constant width. The smooth pleural lobes become narrower and more steeply inclined anteriorly. The border is narrow anterolaterally, widening to about 0·2 mm. at the posterior. Posterolateral spines are not developed.

DISCUSSION. *Sphaeragnostus* is poorly known, the only other possible occurrence in the British Isles being *Sphaeragnostus* sp. from Co. Clare, Ireland (Whittington 1968). However, the presence of the unfurrowed, subcircular, tubercled pygidial axis, and the anterior narrowing of the pleural lobes, would seem to indicate that the Builth specimens belong to this genus.

The species may be distinguished from *Sphaeragnostus similaris* (Barrande 1872) by its more rounded axis. Furthermore, the border, as figured by Barrande (1872, pl. 14, fig. 18), is uniform in width in *S. similaris* whereas it increases in width posteriorly in the Builth specimens. *Sphaeragnostus gaspensis* Cooper & Kindle 1936, differs in that it is appreciably more elongate, the length : width ratio being 1·2 : 1. It also differs in that the axis is more oval; the border however is similar to the Builth specimens in that it increases in width posteriorly. *Sphaeragnostus cingulatus* (Olin 1906) is known from a single poorly preserved specimen in Olin's collection at Lund, and also from one other very poorly preserved specimen probably referrable to this species in the collection at Copenhagen Museum (see Kielan 1960 : 57). The specimens are similar to the Builth ones in that they are less elongate than *S. gaspensis* and have a circular axis, but appear to differ in that the median node is situated very near the anterior margin in *S. cingulatus*. However, until such time as better material is available from Sweden no proper comparison can be made. *Sphaeragnostus* sp. described by Lisogor (1961 : 61) from the Tremadoc of Russia is distinguished in being wider than long, the length : width ratio being 3 : 4. *Sphaeragnostus*? sp. from the Ashgill of Co. Clare, Ireland, is not well documented, but it appears to be more elongate than the Builth form.

The genus exhibits a trend for the pygidium to become more elongate. The earliest-known specimens, from the Upper Tremadoc of Russia, have a length : width ratio of 0·75, whereas in the Ashgill species the ratio is approximately 1·2. The new British species from the Llandeilo together with Barrande's single specimen from Bohemia fit into this trend well with a length : width ratio of about 1·0.

Family **RAPHIOPHORIDAE** Angelin 1854

Genus ***CNEMIDOPYGE*** Whittard 1955

Diagnosis. Cephalon subtriangular to subsemicircular, glabella pyriform with four pairs of muscle areas (these tend to appear as two pairs of " lateral glabellar furrows " on compressed shale specimens); frontal glabellar spine circular in cross section or triangular with ventral side convex and dorsal sides concave, apex running medianly; facial suture just transgresses onto dorsal surface. Thorax rectangular, of six segments, anterior one slightly macropleural. Pygidium triangular, approximately same size as cephalon; axis and pleural fields strongly segmented.

Type species. *Cnemidopyge nuda* (Murchison).

Distribution.—The genus has its maximum development in Britain in the Builth district, being recorded in rocks from lowest Llandeilo to Basal Caradoc age; its only other confirmed British occurrence being as an extreme rarity from the Shelve district. The genus is also present in Sweden and Southern Norway where it ranges in age from Upper Llanvirn (Vikarby Lst.) to Caradoc (Dalby Lst.) (Jaanusson 1960, 1963, 1964). The genus has also been recorded from ?Caradoc rocks of Canada (Norford 1964).

Discussion. Whittard's separation of the genus from *Ampyx* appears well justified, for although the pygidial ribs commonly show irregularities in development, they are persistent throughout all the known species; in addition these form a useful character for species differentiation. However due to the slightly compressed nature of the British material a full definition of the cephalic characters cannot be obtained until the study of the better preserved Scandinavian material at present in hand is completed.

Present knowledge of the genus suggests that it was derived from some, as yet unknown, *Ampyx* in Balto-Scandia by the development of ribs on the pygidium in early Ordovician time, migrated to the Welsh Borderland in Llandeilo time and finally onto N. America in Caradoc time; such migrations are known in Brachiopods (Williams 1969). The differences between some *Ampyx* and *Cnemidopyge* are marginal and there are two species currently placed in *Ampyx*, *A. lobatus* Cooper 1953 from the Porterfield of N. America and *A. salteri* Hicks 1875 from the Arenig of S. Wales, which have some ribs present on the pleural fields. It may be that *A. salteri* was near the ancestral form from which *Cnemidopyge* arose, and that the North American species represents a second, independent development.

Whilst the British representatives of the genus show a progressive increase in the number of pygidial ribs with time, preliminary studies of the Scandinavian forms suggest that this is not the case throughout the genus.

Cnemidopyge nuda (Murchison)

(Pl. 2, figs. 1–8, 10, 12; Pl. 3, figs. 1–5)

1839 *Trinucleus nudus* Murchison : 660, pl. 23, fig. 5.
1849 *Ampyx nudus* (Murchison); Forbes : 1–4, pl. 10, figs. 1–6.
1849 *Ampyx latus* M'Coy : 410.
1851 *Ampyx latus* M'Coy; Sedgwick & M'Coy : 147, pl. 1E, fig. 13.
1851 *Ampyx nudus* (Murchison); Sedgwick & M'Coy : 148.
1925 *Ampyx nudus* (Murchison); Raymond : 31.
1940 *Ampyx nudus* (Murchison); Elles : 406–408, 410–412, 414–419, 421, 432.
1940 *Ampyx nudus* (Murchison); Whittard : 161–162, pl. 5, figs. 9–10.
1940 "*Ampyx*" *latus* M'Coy; Whittard : 162.
1955 *Cnemidopyge nuda* (Murchison); Whittard : 20–21.
1955 *Ampyx latus* M'Coy; Whittard : 21.
1960 *Ampyx latus* M'Coy; Dean : 80.

Diagnosis. *Cnemidopyge* with no median glabellar ridge. Pygidium generally with seven or eight ribs on pleural fields and up to twenty axial rings; pygidia commonly show asymmetrical development of ribs. External surface ornamented with tiny pustules.

Lectotype. GSM. (GSc) 6835 (Pl. 2, fig. 2). Internal mould of cephalon and thorax.

Paralectotype. GSM. (GSc) 6835 (Pl. 2, fig. 1). Internal mould of nearly complete specimen.

Prior to this study, GSM. (GSc) 6835 (originally figured by Murchison 1839, pl. 23, fig. 5), which incorporates two specimens of *C. nuda*, has been loosely referred to as the holotype (Whittard 1940 : 162). It is here proposed to select the specimen consisting of the cephalon and thorax as lectotype and the more complete specimen as paralectotype. Both these specimens are internal moulds and show no trace of the dorsal ornament.

Dimensions.

	A	B	B_1	B_2	I	K	K_1	T.L.
Lectotype	6·7	6·0	4·7	3·9	—	3·5	c. 1·8	—
Paralectotype	—	—	—	—	11·8	4·0	c. 2·0	17·5

	Q	Q_1	R_1	R_2	R_3	R_4
Lectotype	5·3	1·1	11·3	2·3	2·1	11·7
Paralectotype	5·8	1·3	12·0	2·5	2·0	12·3

	W	X	X_1	Z	Z_1	No. of axial rings	No. of ribs Left	No. of ribs Right
Paralectotype	11·3	1·8	0·8	5·9	3·2	11+	7	7

All measurements in mm. For explanation of symbols see Text-fig. 4.

Type locality and horizon. The species was originally described by Murchison (1839 : 660) as from " Gwern-y-fad " and " The Gilwern Hill, Nr. Llandrindod ". The present study however suggests that the species is not present at " Gwern-y-fad ". Forbes (1849 : 1–4) when redescribing the species, states that it was known only from the " Cardeddau Hills, Nr. Builth ", although judging from lithology GSM. 82854, which was probably that figured by Forbes, is almost certainly from Harper's Quarry, north-east of Wellfield. Murchison's original specimen, GSM. (GSc) 6835 bears a label stating that it is from " Pen Carrig, Builth ". Thus some confusion exists as to the type locality, but it is most likely that the type specimens are from the quarry at the south-western end of Pen-cerig Lake, from beds of uppermost Llandeilo age, a supposition that is supported on lithological grounds.

Other figured material. It. 2683 (Pl. 3, fig. 1); It. 2684 (Pl. 2, fig. 10); It. 2685 (Pl. 3, fig. 3); It. 2687 (Pl. 2, fig. 12); It. 2688 (Pl. 2, fig. 5); It. 2691 (Pl. 2, fig. 8); It. 2692 (Pl. 3, fig. 2); It. 2693 (Pl. 2, fig. 4); GSM. 35388 (Pl. 3, fig. 5); SM. A.15,620 (Pl. 2, fig. 6); BU. 365 (Pl. 2, fig. 3; Pl. 3, fig. 4); BU. 366 (Pl. 2, fig. 7).

Distribution. The species is apparently confined to the Builth region, apart from an unconfirmed report from near Llandeilo (Sedgwick & M'Coy 1851 : 148). It is common in the upper part of the Llandeilo, and present as a rarity in the Basal Caradoc.

Description. Complete individuals are ovate, ranging from slightly longer than wide to about one and a half times as long as wide. The extreme cases almost certainly result from a certain amount of compression either parallel or perpendicular to the sagittal line.

The cephalon is subsemicircular in outline, the maximum width being about two and a half times the sagittal length (excluding the frontal glabellar spine). The glabella is pyriform, narrow posteriorly, expanding frontally to about twice the width to form a prominent frontal glabellar lobe. The posterior of this lobe is defined by a pair of " lateral glabellar furrows " which are directed posteromedianly at about 45° and extend about half-way to the sagittal line. Comparison with undistorted limestone material suggests that these furrows are formed by the buckling of the exoskeleton along the line of the *2*p muscle area and more anterior muscle areas (Pl. 2, figs. 9, 11). The posterior pair of " lateral glabellar furrows ", occurring about three-quarters the way along the glabella from the anterior, are continuous, though shallow, medianly, and are similarly believed to have been caused by compression in the region of the *1*p muscle area. Such compression is also believed to account for the isolation from the glabella of the lobes apparently developed laterally to the glabella (the ala of Whittard 1955 : 19, 22; 1966 : 268) (see also Whittington 1959 : 461). The occipital ring is very short (*sag.*), separated from the glabella by a wide, rather shallow furrow. Anteriorly a median glabellar spine is developed which arises from near the top of the steeply declined frontal face of the glabella. In cross section the spine is circular and is generally slightly shorter than the remainder of the cephalon, although on one specimen it is about one and a third times as long.

The genal regions are essentially gently convex, becoming steeply declined laterally and sloping steeply into the deep axial furrows medianly. The posterior border furrow is moderately wide, shallow, and is a direct continuation of the occipital furrow. Its posterior edge is sharply turned up dorsally forming the posterior border. At the genal angles both the border and the border furrow are deflected posterolaterally to form a spatulate projection, the edges of which mark the course of the facial suture where it cuts across the base of the librigenal spines (Pl. 2, fig. 4). The facial suture is marginal frontally, but curves up onto the steep outer regions of the genae laterally, becoming near marginal just before the genal angles prior to cutting across the base of the genal spines. The librigenae are thus confined to a small area on the declined outer parts of the genal regions. A straight, unbranched genal ridge is present commencing opposite the " anterior lateral glabellar furrows " and terminating in the genal angle (Pl. 3, fig. 5). The librigenal spines are long and slender, initially directed posterolaterally, but rapidly becoming more or less posteriorly directed to extend well beyond the pygidium (Pl. 3, fig. 1).

The cephalic doublure is narrow, flat and nearly parallel sided, but medianly invaginated by the hypostomal suture (Pl. 3, fig. 2). A similar structure is known in *Lonchodomas carinatus* Cooper 1953 (see Whittington 1959 : 476, text-fig. 8c, pl. 32, figs. 2, 3). No median suture is present. The hypostoma is unknown.

The thorax is approximately rectangular with the anterior of the six segments being slightly macropleural. The maximum width, generally occurring along the anterior edge of the third segment, is about twice the total sagittal length (see Table 9). The well-defined axis is transversely convex, with only slight tapering posteriorly. Prominent nodes at the anterolateral corners of each axial ring are separated from the main part of the ring by a shallow furrow which merges anteriorly with the pronounced articulating furrow (Pl. 3, fig. 5). The anterior segment is distinct from the other segments in its longer (*exsag.*) pleurae and oblique, not truncated, extremities. The pleural furrow of the anterior segment is slightly sigmoidal, as are those of the remaining segments, although these cut the lateral edge medianly rather than posteriorly. The swollen inner portion of the posterior band is most pronounced in the anterior segment.

The triangular pygidium is about twice as wide as long. The axis is convex, tapering posteriorly but becoming subparallel-sided at the rear, and extends to the posterior margin. Up to 20 axial rings may be developed, although only the anterior nine or ten are generally clearly defined. Occasional specimens (Pl. 3, fig. 5) show paired subcircular muscle scars in the outer parts of the axial ring furrows. Excluding the anterior border, the pleural fields typically possess seven ribs, but show some variation (see Tables 10 and 11). Posteriorly there is a small unfurrowed triangular terminal area. About one-quarter of the specimens show asymmetrical or irregular development of the pleural ribs (Pl. 2, fig. 10). Subparallel terrace lines are present on the ventrally deflected posterolateral borders.

With the exception of parts of the genae, the entire dorsal exoskeleton is ornamented with small pustules about 0·05 mm. in diameter (Pl. 3, figs. 3, 4).

ONTOGENY. A single meraspid specimen about 3·2 mm. long and 3·1 mm. wide most likely belongs to degree 5 (Pl. 2, fig. 7), but due to disturbance of the thorax the exact number of segments is uncertain, and although there are apparently only four segments on the axis, the pleural regions suggest five. The cephalon is similar to that of the adult form; the glabella however is carinate, a feature possibly accentuated by compression, while the " lateral glabellar furrows " are lacking. The frontal glabellar spine is about two-thirds the cephalic length. The genal regions are rather flat, and apart from the lack of genal ridges are similar to those of holaspides.

The thoracic segments are poorly preserved but appear to resemble those of the adult.

The transitory pygidium is triangular, possibly slightly more obtusely rounded posteriorly than in the holaspid. Only four, or possibly five ribs are developed on the pleural fields with only about six or seven axial rings discernible.

BIOMETRICAL DATA. Relatively few complete specimens are known and estimated length : width ratios were possible in only five specimens (see Table 6). Although the values vary considerably they provide no real evidence of the existence of two distinct forms as recorded by Whittard (1955) in some raphiophorids. It is believed that

TABLE 6

Total length	Width	Length/Width
c. 11·0	10·4	c. 1·06
c. 13·5	9·0	c. 1·50
c. 17·0	13·8	c. 1·23
17·5	11·3	1·55
c. 22·0	17·0	c. 1·30

Length and width measurements for complete specimens of *C. nuda* (Murchison). All measurements in mm. and taken on internal moulds.

TABLE 7

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : K	5·47	0·9555	4·04	0·3664	0·764	0·770	0·84	0·0286	0·62	0·01597	12
$K : K_1$	4·07	0·5540	2·02	0·0940	0·939	0·942	0·83	0·0194	0·41	0·00502	6
$B : B_1$	5·84	1·5331	4·58	1·0354	0·987	0·987	1·05	0·0023	—	—	14
$B : B_2$	5·86	1·6508	3·68	0·7483	0·984	0·983	1·07	0·0035	0·67	0·00131	13

Bivariate statistics for the cephalon of *C. nuda* (Murchison). All measurements in mm. For explanation of symbols see Text-figs. 4.

TABLE 8

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	14·41	8·9012	6·48	1·7050	0·928	0·932	0·97	0·0178	0·44	0·00380	9
W : X	14·11	8·8189	2·34	0·2956	0·954	0·955	1·10	0·0133	0·18	0·00038	10
Z : X	6·25	1·5400	2·42	0·2000	0·850	0·850	0·93	0·0172	0·36	0·00257	16
$X : X_1$	2·54	0·2400	1·22	0·1178	0·914	0·918	1·44	0·0408	0·22	0·00124	10
$Z : Z_1$	6·12	1·9543	3·77	0·9464	0·942	0·943	1·13	0·0108	0·70	0·00419	15

Bivariate statistics for the pygidium of *C. nuda* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 9

Q	Q_1	R_1	R_2	R_3	R_4
—	—	c. 15·4	3·4	2·7	c. 15·6
—	1·3	—	4·0	—	—
7·3	1·5	—	—	—	—
—	1·3	—	3·3	—	—
10·2	1·2	—	—	—	—
5·3	1·1	11·3	2·3	2·1	11·7
5·8	1·3	12·0	2·5	2·0	12·3

Thoracic measurements for *C. nuda* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 10

	Complete specimens				
Number of ribs . . .	6	7	8	Asymmetrical	Irregular
Number of specimens . .	0	13	7	5	2
	Left pleural fields				
Number of ribs . . .	6	7	8	Irregular	
Number of specimens . .	1	18	10	0	
	Right pleural fields				
Number of ribs . . .	6	7	8	Irregular	
Number of specimens . .	2	20	8	3	

Full data of rib counts on the pleural fields of *C. nuda* (Murchison).

TABLE 11

Number of ribs	6	7	8
Number of specimens	2	21	12

mean = 7·29; var. = 0·3276; n = 35

Frequency distribution of the number of ribs on the pleural fields of *C. nuda* (Murchison), together with the mean and variance.

the variation in the length : width ratios are due to the combination of individual variation coupled with the effects of slight compression.

From Table 10 it is seen that only 5 % of the total number of pleural fields show irregularities in rib development. Counts on complete pygidia reveal that 7·5 % show irregularities in rib development, while a further 18·5 % of the total number of specimens show more ribs on one pleural field than on the other. In order to calculate the mean number of ribs developed using as large a sample as possible, the data for the right field alone were considered, except in cases where data were only available for the left field; thus only one field was considered on any given specimen. The data obtained are given in Table 11. A 2 × 2 probability test shows that there is no significant correlation between the number of ribs developed and the length of the pygidium, and thus there is no necessity to relate rib counts to the size of the individual.

DISCUSSION. *C. nuda* is characterized by the number of ribs on the pygidium and the lack of a median glabellar ridge and may be distinguished from other *Cnemidopyge* by these two characters. *C. nuda granulata* Whittard 1955 has a slightly more coarsely developed surface ornament. The various Scandinavian forms appear to have a different surface ornament, possibly a reflection of a differing environment, and also generally possess a weak median glabellar ridge.

Re-examination of specimen SM. A.15620, described as *Ampyx latus* by M'Coy (1849 : 410) and Sedgwick & M'Coy (1851, pl. 1E, fig. 13), shows that six thoracic segments are present and not five as had previously been thought. The slight overlap of the pygidium onto the posterior of the thorax partially obscures the sixth segment, but the sixth axial ring and part of the right pleura are clearly visible (Pl. 2, fig. 6). The specimen is identical to the small specimens of *C. nuda* found at the eastern end of the stream exposures east of Tre coed, north of Builth, and *A. latus* M'Coy is accordingly included here in the synonymy of *C. nuda*.

Although recorded from the Shelve region in the past, Whittard (1955 : 20) has given reasons for supposing these to be due to mis-labelling of specimens and thus the species appears to be restricted to the Builth region.

Slight swellings on the genal ridge described by Sedgwick & M'Coy (1851 : 148) and thought by them to be rudimentary eyes have not been observed. However the preliminary studies of the Scandinavian species reveals the presence of a genal caecal system based on a main caeca correspondingly situated to the genal ridge of *C. nuda*, and any swellings along the ridge are presumed to be related to this caecal system rather than to visual organs.

The species varies considerably in size, being significantly larger (size represented by pygidial length) at the exposures above the right bank of the stream 200 yards east of Pen-cerig Lodge, and significantly smaller at the eastern end of the stream section 160 yards south-east of Tre coed than at the type locality (holaspid specimens only taken into consideration).

Cnemidopyge nuda (Murchison) ***granulata*** Whittard

(Pl. 4, figs. 1–6; Pl. 5, figs. 1, 5)

1940 *Ampyx nudus* (Murchison); Elles : *pars*. 408, 412.
1955 *Cnemidopyge granulata* Whittard : 22, pl. 2, figs. 9–12.
1966 *Cnemidopyge granulata* Whittard; Whittard : 268–269, 299, pl. 46, fig. 7.

DIAGNOSIS. *Cnemidopyge nuda* generally with eight ribs on pleural fields. External surface ornamented with small granules.

TYPE MATERIAL. Holotype. GSM. 92950 (Pl. 4, fig. 1; Pl. 5, fig. 5). Internal and external moulds of cranidium.

Paratype. GSM. 92951 (Pl. 4, fig. 3). Internal and external moulds of incomplete thorax and pygidium.

DIMENSIONS. Owing to the incomplete and distorted nature of the type specimens very few measurements can be made. However, estimates of various measurements have been made as follows:

	A	B_1	I	K	K_1
Holotype	11·0	8·0	24·0	8·5	4·0

	Q	Q_1	R_1	R_2	R_3	R_4	W	Z
Paratype	11·1	2·7	33·5	7·5	6·0	33·0	32·0	12·5

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITY AND HORIZON. Both specimens are from near the base of the Rorrington Beds of the Holywell Burn, the holotype from The Mount, near Rorrington, Shropshire, and are of Upper Llandeilo age (see Williams 1969a).

OTHER FIGURED MATERIAL. It. 2702 (Pl. 4, fig. 4); It. 2703 (Pl. 4, fig. 6); It. 2704 (Pl. 4, fig. 2); It. 2705 (Pl. 4, fig. 5; Pl. 5, fig. 1).

DISTRIBUTION. The subspecies is known from both the Shelve and Builth regions. At Shelve it is exceedingly rare, being known from only three specimens ranging in age from Upper Llandeilo to lowest Caradoc. Although by no means common, the subspecies is slightly more abundant at Builth being known from about twenty specimens from beds of probable Upper Llandeilo age.

DESCRIPTION. On account of the close affinity to *C. nuda s.s.* only a comparative description is given together with some revision of Whittard's original definition.

Whittard's description was based on very limited material, and it is now known that several features described by him are liable to some variation. The cephalon is extremely similar to that of *C. nuda*, the protuberant glabella described by Whittard is considered to be the result of slight buckling of the steep outer portions of the genal regions. Further, the cephalic width may vary from just under two and a half times to about two and three-quarter times the length, while the axial furrows may be as deep, or deeper than the posterior border furrow. Unlike *C. nuda* no trace of any genal ridge has been detected. A granular surface ornament is developed and as in *C. nuda* this is most coarsely developed on the glabella; the granules are, however, somewhat larger than in *C. nuda*, ranging from 0·06 mm. to 0·08 mm. in diameter (Pl. 5, fig. 1). This coarser granulation typifies the thorax and pygidium (Pl. 4, fig. 5).

The pygidium shows some interesting minor differences from *C. nuda*, for although the numbers of ribs on the pleural fields overlap, the mean is slightly, though significantly higher in *C. nuda granulata* (see Table 13). Further, although relatively few specimens are available, irregular rib development is so far unknown in *C. nuda granulata*.

Ontogeny. Meraspis ?Degree 3. One poorly preserved specimen (Pl. 4, fig. 6) about 1·6 mm. long and 1·9 mm. wide appears to have only three thoracic segments. The associated left genal region is smooth and without a genal ridge. The thoracic segments appear to conform to the general raphiophorid pattern. The triangular pygidium is rather shorter and more obtusely rounded posteriorly than in adult specimens. The pleural fields are furrowed, and although the total number of ribs is not discernible it is certainly less than in the holaspid form.

Biometrical data. Although more material is known from Builth than from the type locality, data are insufficient for formal analysis. It is worth noting that the Builth specimens are smaller than the type specimens, being more comparable in size with the third specimen from Shelve, GSM. 102174 (Whittard 1966; pl. 46, fig. 7). The few data for the ribs of the pleural fields of the Builth material are given in Table 12.

Table 12

Complete specimens

Number of ribs	7	8	9	Asymmetrical
Number of specimens	1	3	1	1

Frequency distribution of the number of ribs on the pleural fields of complete specimens of *C. nuda* (Murchison) *granulata* Whittard together with the incidence of pygidia showing asymmetrical development of ribs.

No specimen has irregular development of ribs. Considering data for the right field only, except where data are only available for the left field, the distribution is as in Table 13.

A 2×2 probability test shows that there is no significant correlation between the number of ribs developed on the pleural fields and the length of the pygidium.

TABLE 13

Number of ribs	7	8	9
Number of specimens . . .	2	4	1

mean = 7·86; var. = 0·476; n = 7.

Frequency distribution of the number of ribs on the pleural fields of *C. nuda* (Murchison) *granulata* Whittard together with the mean and variance.

Comparison of the corresponding data for *C. nuda* and *C. bisecta* shows that the mean number of ribs for *C. nuda granulata* falls between those of the other species. Application of the " t " test however shows the difference in the means of *C. nuda* and *C. nuda granulata* to be significant at the 5% level ($0{\cdot}05 > P > 0{\cdot}01$), but that there is no significant difference between the values for *C. nuda granulata* and *C. bisecta*.

DISCUSSION. When Whittard first described this species (1955 : 22) it was not known that the other species of *Cnemidopyge* also possessed a granular surface ornament. The present study, while indicating that *C. nuda granulata* is morphologically distinct from *C. nuda s.s.* in that the surface ornament is more coarsely developed, suggests that the degree of morphological similarity is too great to warrant the continued specific separation of these two forms.

The other two species, *C. parva* sp. nov. (see below) and *C. bisecta* are readily distinguished, the former by its smaller number of pygidial ribs and fine surface ornament and the latter by its prominent median glabellar ridge.

C. nuda granulata continues the trend seen in *C. parva* and *C. nuda* for the number of pygidial ribs to increase with time. It also is the oldest British *Cnemidopyge* to exhibit the coarser ornament which becomes well developed in *C. bisecta*.

The subspecies, which occurs at approximately the same horizon both at Builth and Shelve, is short lived, apparently giving rise to *C. bisecta* with the appearance of the median glabellar ridge.

Cnemidopyge parva sp. nov.

(Pl. 4, fig. 7; Pl. 5, figs. 2–4, 6–8; Pl. 6, fig. 1; Pl. 7, fig. 4)

1940 *Ampyx nudus* (Murchison); Elles : *pars*. 406–407, 410, 412.

DIAGNOSIS. *Cnemidopyge* generally with only five or six ribs developed on pleural fields. Glabella with no median ridge.

TYPE MATERIAL. Holotype. It. 2694 (Pl. 6, fig. 1). Internal mould of nearly complete specimen.

Paratypes. It. 2695 (Pl. 5, figs. 4, 8). External mould of damaged cephalon. It. 2696 (Pl. 7, fig. 4). Internal and external moulds of damaged, nearly complete specimen. It. 2697 (Pl. 4, fig. 7). Internal mould of cephalon with frontal glabellar spine. It. 2698 (Pl. 5, fig. 7). Internal mould of pygidium.

DIMENSIONS.

	A	A_1	B	K	Q	Q_1	R_1	R_2	R_3	R_4
Holotype	—	—	—	c. 5·0	5·3	1·2	13·0	3·6	2·7	13·0
It. 2697	5·3	4·4	4·8	3·5	—	—	—	—	—	—

	W	X	X_1	Z	Z_1	No. of axial rings	No. of ribs Left	No. of ribs Right	T.L.
Holotype	11·8	2·4	1·3	5·2	3·0	14+	5i	6	c. 16·5
It. 2698	10·6	2·2	0·8	5·0	2·8	12+	5	5	—

All measurements in mm. For explanation of symbols see Text-fig. 4. "i" indicates an additional incipient rib.

TYPE LOCALITY AND HORIZON. Shales of Llandeilo age in the left bank of the stream section east of Bach-y-graig, 40 yards east of the point where the footpath enters the wood at the western end of the section.

OTHER FIGURED MATERIAL. It. 2699 (Pl. 5, fig. 2); It. 2700 (Pl. 5, fig. 3); It. 2701 (Pl. 5, fig. 6).

DISTRIBUTION. Apart from the type locality the species is also known from the stream section west of Wellfield Lodge immediately below the point where the stream is piped under the road; age similar to that of the type locality.

DESCRIPTION. A full description of this species is superfluous as it differs from *C. nuda* (Murchison) described above mainly in the pygidium, which has only five or six ribs on the pleural fields with 14 or 15 axial rings (Pl. 6, fig. 1). A possible difference in the thorax is that the axis of the new species may be relatively wider anteriorly than in the other British species (cf. Tables 9, 14, 19).

A solitary librigena (Pl. 5, fig. 2) is very like that deduced for *C. nuda* being small, fused posteriorly into the librigenal spine and clearly restricted to a small area on the lateral portions of the genal regions.

ONTOGENY. Degree unknown. A disarticulated specimen of a compressed cephalon and a small transitory pygidium is known (Pl. 5, fig. 6). The transitory pygidium is smaller than that of a possible meraspid degree 2 specimen, but is essentially similar to the adult form. The posterior is however more obtusely rounded, and fewer axial rings are developed.

?Degree 2. A single poorly preserved specimen (Pl. 5, fig. 3) has apparently only two thoracic segments. It appears very similar in basic morphology to the adult form, but preservation is insufficient to allow detailed comparisons. Four and five pygidial ribs are developed on the left and right pleural fields respectively.

BIOMETRICAL DATA. Relatively few specimens of this new species are known and thus few data are available; such as are, are included in Tables 14–17.

As regards the rib counts it is seen that of the specimens upon which complete counts were possible, one-quarter are asymmetrical, with equal numbers of the

TABLE 14

Q	Q_1	R_1	R_2	R_3	R_4
5·3	1·2	13·0	3·6	2·7	13·2
—	1·3	11·3	c. 3·0	2·4	11·5
—	0·8	9·5	2·5	—	9·7

Thoracic measurements on *C. parva* sp. nov. All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 15

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	9·22	7·7200	3·87	2·3171	0·990	0·992	1·29	0·00438	—	—	8
W : X	9·22	7·7200	1·89	0·3214	0·988	0·990	0·98	0·00346	0·20	0·00166	8
Z : X	3·87	2·3171	1·89	0·3214	0·985	0·988	0·78	0·00239	—	—	8
Z : Z_1	4·25	2·2767	2·55	0·6967	0·992	0·993	0·93	0·00599	0·55	0·00214	4

Bivariate statistics for the pygidium of *C. parva* sp. nov. All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 16

	Right pleural field		
Number of ribs	4	5	6
Number of specimens	—	5	4
	Left pleural field		
Number of ribs	4	5	6
Number of specimens	1	5	3
	Complete specimens		
Number of ribs	5	6	Asymmetrical
Number of specimens	3	3	2

Full data on rib counts on the pleural fields of *C. parva* sp. nov.

TABLE 17

Number of ribs	4	5	6
Number of specimens	—	6	4

mean = 5·40; var. = 0·267; n = 10

Frequency distribution of the number of ribs on the pleural fields of *C. parva* sp. nov., together with the mean and variance.

remainder having five or six ribs. Data obtained by considering counts on the right pleural field, except where data are only available for the left, being given in Table 17.

The few cephalic measurements obtained show no obvious difference from those of *C. nuda*. The various thoracic measurements for *C. parva*, *C. nuda*, and *C. bisecta* show that there are virtually no differences between these species with regard to the overall outline, relative length (*exsag.*) of the anterior segment or the tapering of the axis. Despite the general lack of data, it appears that the anterior of the axis may be relatively wider in *C. parva* than in the other species. Analysis of data for the pygidium shows that although no difference is recognizable in shape *C. parva* is readily distinguished by having significantly fewer ribs.

DISCUSSION. This new species represents the earliest *Cnemidopyge* known from the British Isles. It may be distinguished from *C. bisecta* (Elles) by its lack of median glabellar ridge, and from both *C. nuda* and *C. nuda granulata* by the smaller number of ribs developed on its pleural fields. It is also noteworthy that of a total of eighteen counts, no examples of irregular ribbing have been observed in *C. parva*, although one-quarter of individuals have one more rib on one pleural field than on the other. In *C. nuda* 5% of pleural fields show irregular development of ribs, and in *C. bisecta* the figure is as high as 28%.

Cnemidopyge bisecta (Elles)

(Pl. 6, figs. 2–9; Pl. 7, figs. 1–3, 5; Pl. 8, fig. 3)

1940 *Ampyx bisectus* Elles : *pars*. 416–419, 421–422, 432, pl. 29, figs. 1–5.
1955 *Cnemidopyge bisecta* (Elles); Whittard : 15, 21.

DIAGNOSIS. *Cnemidopyge* having median glabellar ridge, merging anteriorly with frontal glabellar spine. Pygidium with generally eight or nine pleural ribs commonly showing asymmetrical or irregular development of ribs. Dorsal surface of exoskeleton ornamented with small granules.

TYPE MATERIAL. Holotype. SM. A.10,073 (Pl. 8, fig. 3). Internal mould of nearly complete specimen.

Paratypes. SM. A.10,074 (Pl. 6, fig. 4). Internal mould of large cephalon. SM. A.10,075. Internal mould of damaged specimen lacking pygidium. SM. A.10,076. Internal mould of damaged specimen lacking pygidium. SM. A.10,077. Internal mould of cephalon.

DIMENSIONS.

	A	A_1	B	B_1	B_2	I	K	K_1
Holotype	8·1	—	7·6	5·6	4·4	17·9	6·5	3·9
SM. A.10,074	14·4	—	12·7	10·1	8·2	27·3	9·7	5·7
SM. A.10,075	10·0	*c.* 7·0	9·0	6·6	5·1	—	7·5	—
SM. A.10,076	8·4	—	7·9	6·0	4·9	—	5·8	3·8
SM. A.10,077	7·8	—	6·8	5·4	4·4	16·6	6·5	3·9

	Q	Q_1	R_1	R_2	R_3	R_4
Holotype	7·1	1·6	18·5	4·4	3·6	19·5
SM. A.10,075	9·1	2·0	—	—	—	—
SM. A.10,076	6·9	1·6	—	4·3	3·3	—

	W	X	X_1	Z	Z_1	No. of axial rings	No. of ribs Left	No. of ribs Right
Holotype	18·0	3·3	1·5	6·9	4·9	9+	8*	7

All measurements in mm. For explanation of symbols see Text-fig. 4.

* Pleural furrow separating 7th and 8th ribs developed only at lateral and axial extremities.

TYPE LOCALITY AND HORIZON. Dark shales beneath the dolerite in the middle quarry, Llanfawr, Llandrindod, of Basal Caradoc age (*gracilis* Zone).

OTHER FIGURED MATERIAL. It. 2707 (Pl. 6, fig. 9); It. 2708 (Pl. 6, fig. 5); It. 2710 (Pl. 6, fig. 2); It. 2711 (Pl. 6, fig. 6); It. 2712 (Pl. 7, fig. 1); It. 2713 (Pl. 6, fig. 7); It. 2714 (Pl. 7, fig. 3); It. 2715 (Pl. 7, fig. 5); It. 2716 (Pl. 6, fig. 8); It. 2717 (Pl. 7, fig. 2); I. 4289 (Pl. 6, fig. 3).

DISTRIBUTION. The species is apparently confined to the Builth-Llandrindod region. Despite records by Elles (1940 : 408, 412, 432) of its occurrence in the highest Llandeilo, the present study indicates that it is restricted to the Basal Caradoc.

DESCRIPTION. Although readily distinguished, this species is similar to *C. nuda* except for a few features, and requires only a comparative description.

The few known complete specimens are about one and a quarter times as long as wide and are thus comparable to *C. nuda*.

The most striking difference in the cephalon is the presence of the median glabellar ridge commencing immediately in front of the " *1*p furrows " and fusing frontally with the base of the frontal glabellar spine. The " *1*p furrows " are shallow medianly (Pl. 6, fig. 4) resulting in the " basal glabellar lobe " being less clearly defined anteriorly than in *C. nuda*. The posterior border furrow deepens distally to form a shallow depression at the base of the librigenal spine. The librigenal spines are long, slender and gently curved initially, becoming straight and posteriorly directed, extending well beyond the pygidium (Pl. 6, fig. 3). The course of the facial suture is a little obscure but it may not encroach very high on to the dorsal surface laterally. The cephalic doublure and hypostoma are not known.

The granular surface ornament is distributed in a basically similar manner to that in *C. nuda*, but an extra band of tiny pustules, about 0·04 mm. in diameter, is developed just anterior of the posterior border furrow (Pl. 7, fig. 5). The granules on the glabella are about 0·09–0·10 mm. in diameter, while those on the genae are only about 0·05–0·07 mm.

Apart from the surface ornament the thorax is similar to that of *C. nuda*. The granular ornament is coarser and also is well developed along the anterior edge of the anterior pleural band and on the posterior pleural band, but is absent in the pleural furrow (Pl. 6, fig. 9).

The pygidium is similar to that of *C. nuda* but differs in that the mean number of ribs is significantly higher in *C. bisecta*. There is also a much higher incidence of irregularities in the rib development than in *C. nuda* (28 %, 5 %; see also pages 68, 77). In common with the remainder of the dorsal exoskeleton the ornamentation is more coarsely developed in *C. bisecta*.

BIOMETRICAL DATA. More data are available for *C. bisecta* than for other species of *Cnemidopyge*. Although the species is abundant, complete individuals are very rare, two only providing length : width ratios of between 1·2 and 1·3.

The relatively complete data have enabled a number of bivariate analyses to be carried out on the cephalon, thorax and pygidium. The statistics obtained from these are given in Tables 18–22.

Table 18

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var α	a	var. a	n
I : B	17·60	28·5200	7·73	7·2140	0·994	0·994	1·14	0·0039	0·50	0·00076	6
B : K	8·10	2·4855	6·44	1·5427	0·915	0·914	0·99	0·0161	0·79	0·01010	12
K : K_1	6·40	1·7133	3·53	0·8533	0·949	0·951	1·27	0·0193	0·71	0·00619	10
B : B_1	8·10	2·2385	6·29	1·4831	0·984	0·984	1·05	0·0029	0·81	0·00175	14
B : B_2	8·19	2·2958	5·08	1·0267	0·972	0·972	1·08	0·0058	0·67	0·00224	13

Bivariate statistics for the cephalon of *C. bisecta* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 4.

Table 19

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
R_1 : Q	18·70	2·0150	7·62	0·5675	0·877	0·875	1·30	0·1316	0·53	0·02167	5
R_1 : R_2	17·45	14·0270	4·05	1·2350	0·906	0·909	1·27	0·0699	0·30	0·00394	6
R_2 : R_3	4·40	0·4160	3·65	0·3310	0·963	0·963	1·07	0·0210	0·89	0·01449	6
Q : Q_1	7·73	0·8150	1·66	0·0667	0·887	0·887	1·33	0·0733	0·29	0·00349	7

Bivariate statistics for the thorax of *C. bisecta* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 4.

Table 20

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	17·72	11·2433	7·74	3·0875	0·941	0·942	1·19	0·0146	0·52	0·00286	13
W : X	17·72	11·2433	3·15	0·4375	0·959	0·962	1·10	0·0083	0·20	0·00028	13
Z : X	8·11	3·6041	3·23	0·4268	0·912	0·916	0·87	0·0058	0·34	0·00095	23
X : X_1	3·15	0·4539	1·32	0·0472	0·883	0·883	0·77	0·0077	—	—	19

Bivariate statistics for the pygidium of *C. bisecta* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 4.

Table 21

			Complete specimens			
Number of ribs . . .	7	8	9	10	Asymmetrical	Irregular
Number of specimens . .	—	4	3	—	3	7
			Left pleural field			
Number of ribs . . .	7	8	9	10	Irregular	
Number of specimens . .	—	9	3	—	7	
			Right pleural field			
Number of ribs . . .	7	8	9	10	Irregular	
Number of specimens . .	2	9	5	1	5	

Full data of rib counts on the pleural fields of *C. bisecta* (Elles).

TABLE 22

Number of ribs . . .	7	8	9	10
Number of specimens . .	6	13	7	1

mean = 8·11; var. = 0·6410; n = 27

Frequency distribution of the number of ribs on the pleural fields of *C. bisecta* (Elles), together with the mean and variance.

Of the total number of pleural fields for which data are available, 28% show irregularities in rib development. Of the complete specimens known 41% show some rib irregularities and a further 18%, although showing no irregular ribs, possess more ribs on one field than on the other. Table 22 shows the data for right fields only, except in cases where data are available for the left field only. A 2 × 2 probability test again reveals that there is no significant correlation between the number of ribs and the pygidial length.

Tests show that, where bivariate analyses of relative growth and shape are available, the three species of *Cnemidopyge*, *C. bisecta*, *C. nuda* and *C. parva* are fundamentally alike. Indeed *C. bisecta* differs significantly from the other two only in the number of ribs developed on the pleural fields, in the occurrence of irregularities in rib development and such non-parametric features as surface ornament.

DISCUSSION. In her original description, Elles (1940 : 422) implied that a triangular pygidium was only characteristic of *C. bisecta*. In fact the pygidial outline of *C. nuda* is indistinguishable from that of *C. bisecta*, and it is possible that reliance on this alleged difference led Elles to misidentify *Cnemidopyge* found in the uppermost Llandeilo as belonging to *C. bisecta*.

C. bisecta is easily distinguished from *C. parva* sp. nov. by its greater number of pygidial ribs and the possession of a median glabellar ridge. *C. nuda* (Murchison) may be distinguished by the lack of median glabellar ridge.

C. bisecta shows the culmination of the two trends, i.e. pygidial rib numbers and granulation. The presence of the median glabellar ridge in *C. bisecta* is of some interest as it appears to be present, though not so prominent, in the Scandinavian representatives of the genus.

Although some of the irregularities in the rib development on the pygidium may be pathological (Pl. 7, fig. 2), the incidence of irregularities is unusually high and may represent an inherited characteristic.

Raphiophorid sp. indet.

(Pl. 8, figs. 1, 2)

FIGURED SPECIMEN. It. 2718. External mould of damaged cranidium and anterior part of thorax.

LOCALITY AND HORIZON. From Lower Llanvirn shaly mudstones exposed in the Camnant Brook, probably from above Court.

DESCRIPTION. The cephalon is about two and a half times as wide as long and is similar to that of *C. nuda*. The glabella is clavate, with no median ridge and possesses a frontal spine which is circular in cross section. The glabellar segmentation appears to be similar to that of other raphiophorids. The genal regions are gently tumid except for their outer portions which are more steeply declined. No trace of any surface ornament or genal ridges is present.

The anterior three thoracic segments are present, though poorly preserved. The anterior one is slightly macropleural and they all appear to be typically raphiophorid.

The pygidium is not known.

Discussion. Although poorly preserved, this specimen is of interest as it is the only confirmed occurrence of a raphiophorid from the Llanvirn of the Builth region. Elles records *Ampyx salteri* Hicks 1875 as an extreme rarity from the "*Trinucleus*" band in the upper part of the Lower Llanvirn (Elles 1940 : 395). This specimen has not been traced and its identification is open to question.

The raphiophorid species typical of the equivalent horizon in the Shelve region is *Ampyx linleyensis* Whittard 1955, and although no proper comparison can be made, the cephalon of the Builth specimen does appear less triangular than that of *A. linleyensis*.

Family **CHEIRURIDAE** Salter 1864
Subfamily **CYRTOMETOPINAE** Öpik 1937
Genus ***PLACOPARINA*** Whittard 1940

Diagnosis. Cyrtometopinid having pedunculate eyes situated close to anterior of cephalon, associated with transverse structures very like eye ridges; long (*exsag.*) narrow (*tr.*) librigenae, almost gonatoparian facial sutures; short transversely directed fixigenal spines. Glabella with three pairs subequal lateral furrows. Thorax of twelve segments. Pygidium with three pairs of pleural spines.

Type species. *Placoparina sedgwickii sedgwickii* (M'Coy).

Distribution. The genus is not known outside England and Wales and is apparently confined to *P. sedgwickii sedgwickii* (M'Coy) from the Llandeilo of the Builth inlier and *P. sedgwickii* (M'Coy) *shelvensis* subsp. nov. from the highest Lower Llanvirn of the Shelve region. In addition it has been recorded from beds of uncertain age from Abereiddy Bay and it may also be present in the Skiddaw Slates (Whittard 1958 : 115).

Discussion. Whittard originally erected this genus for *Cryphaeus sedgwickii* M'Coy which he separated from *Eccoptochile* Hawle & Corda 1847 on account of its blindness. Prantl & Přibyl (1947 : 25) and Přibyl (1953 : 39) did not accept that the blindness of *P. sedgwickii* warranted its generic separation from *Eccoptochile* and accordingly they rejected *Placoparina*. Whittard (1958 : 113–115), however, described eyes from new material of *P. sedgwickii* and thus the status of *Placoparina* clearly demanded reconsideration. Whittard was able to show that although eyes were present, other newly discovered features, notably the long (*exsag.*) narrow (*tr.*) librigenae were clearly unlike other known cheirurid genera and warranted the retention of *Placoparina* as a distinct genus. Having regard in particular to the form of the librigenae, situation of the pedunculate eyes and the near gonatoparian condition of the facial sutures it is here proposed to follow Whittard and accord full generic status to *Placoparina*.

Placoparina sedgwickii sedgwickii (M'Coy)

(Pl. 8, figs. 4–6; Pl. 9, fig. 3)

1849 *Cryphaeus Sedgwickii* M'Coy : 406–407.
1851 *Eccoptochile Sedgwickii* (M'Coy); Sedgwick & M'Coy : 155–156, pl. 1F, fig. 14.
1852 *Cheirurus* (*Cryphaeus*) *Sedgwicki* (M'Coy); Barrande : 775.
1854 *Cryphaeus* (*Eccoptochile*) Sedgwickii M'Coy; M'Coy : 145.
1864 *Cheirurus* (*Eccoptochile*) *Sedgwicki* (M'Coy); Salter : 73, pl. 5, fig. 17.
1940 *Placoparina sedgwicki* (M'Coy); Whittard : *pars.* 168, pl. 6, figs. 5, 6; *non* figs. 7–9.
1945 *Cheirurus sedgwickii* (M'Coy); Reed : 59.
1958 *Placoparina sedgwicki* (M'Coy); Whittard : *pars.* 113–115. Includes full synonomy.

DIAGNOSIS. *Placoparina* with well developed terminal axial piece and spatulate terminations to pygidial pleurae.

HOLOTYPE. SM. A.15616a, b (Pl. 8, figs. 4, 5; Pl. 9, fig. 3). Internal and external moulds of damaged entire exoskeleton.

DIMENSIONS. Owing to the damaged nature of this specimen only a limited number of measurements are possible, the details of which are given below.

T.L.	Q	Q_1	R_1	R_2	R_3	R_4	W	X	Y	Z
c. 75·0	40·0	3·6	*c.* 58·0	12·5	8·4	*c.* 49·0	33·0	8·4	10·2	14·3

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITY AND HORIZON. The exact locality of the holotype is not known. It was given imprecisely by M'Coy as " Two miles north of Builth ". Elles believed that this specimen was from the stream section south-east of Tre coed (Elles 1940 : 410), but although this is possible on lithological grounds, prolonged searching has failed to reveal any further specimens. The species is known from only two other localities in the Builth district (on the right bank above the stream 200 yards east of Pen-cerig Lodge and about 80 yards west of the junction of the Cefnllys road and the lane to Gorse farm, this latter locality being no longer accessible due to road improvements) and neither of the lithologies from these localities matches that of the type specimen. Although the exact locality must remain uncertain it is thought most likely to lie within the Llandeilian outcrop.

OTHER FIGURED SPECIMEN. BU. 367 (Pl. 8, fig. 6).

DISTRIBUTION. Only three specimens of this subspecies are known all from the Llandeilo of the Builth region. *P. sedgwicki s.l.* is known from beds of uncertain age from Abereiddy Bay and may also be present in the Skiddaw Slates (see Whittard 1958 : 115).

Description. Complete individuals are subrectangular in outline being about one and a half times as long as wide.

The rounded cephalon is about three and a half times as wide as long. The glabella is convex, defined by deep, slightly outwardly convex axial furrows, and its maximum width is only slightly less than its length. The frontal lobe of the glabella is anterior of the maximum width and by analogy to *P. sedgwickii shelvensis* subsp. nov. (see page 80) is believed to overhang the anterior border furrow. The three pairs of lateral glabellar furrows are curved backwards, *1*p extending towards the occipital furrow; *2*p extend about one-third of the distance across the glabella; while *3*p, although parallel to *2*p, extend for a slightly shorter distance. The occipital ring is well developed and possesses no median node. The fixigenae are large, steeply declined marginally, and are assumed to extend nearly to the lateral cephalic margins, although details of the librigenae are unknown. The posterior border furrow is deep and delimits the prominent convex posterior border. Both the posterior border and the border furrow expand distally. Eyes are not certainly known but are probably situated in a position similar to those of *P. sedgwickii shelvensis*. The surface of the fixigenae is coarsely pitted and finely granular between the larger pits. The pits are lacking on the glabella, which does however retain the fine granular ornament.

The nearly parallel-sided thorax consists of 12 segments. The axis is prominent, occupying about one-fifth of the total thoracic width. The axial rings are simple with weakly developed lateral nodes and well developed articulatory furrows and half rings. The pleural regions are relatively flat, being only slightly arched between the fulcra and the axial furrows. Medianly each pleura is divided into an anterior and posterior band by a line of pits which in larger individuals may be sunken slightly below the level of the remainder of the pleura (Pl. 8, fig. 5). The pits only extend as far as the fulcrum, beyond which the pleurae trend posterolaterally, the deflection becoming progressively greater to the posterior, and terminate in a stout spine. The external surface of the thorax is covered with a fine granular ornament but the sunken granules, described by Whittard (1958 : 114) as becoming progressively more abundant to the posterior in the Shropshire specimens are not developed.

The pygidial axis consists of three prominent axial rings and a well developed triangular terminal piece which reaches the margin medianly. The anterior pleurae are similar to those of the thorax and possess a median transverse line of pits. Distally, however, they form spatulate posteriorly directed pleural terminations. The second pair are smaller, have fewer pits developed medianly, but terminate similarly. The third pair are much reduced and have only two pits developed medianly, but again possess well developed spatulate terminations. The external surface is ornamented with fine granules but as in the thorax the sunken granules described by Whittard are absent.

Discussion. See discussion of *P. sedgwickii* (M'Coy) *shelvensis* subsp. nov.

Placoparina sedgwickii (M'Coy) ***shelvensis*** subsp. nov.

1940 *Placoparina sedgwickii* (M'Coy); Whittard : *pars*. 166–169, pl. 6, figs. 7–9.
1958 *Placoparina sedgwicki* (M'Coy); Whittard : *pars*. 113–115, pl. 15, figs. 6–13.

Diagnosis. *P. sedgwickii* having sunken granules on external surface of thorax and pygidium, and less spatulate terminations to third pygidial pleura.

Type material. Holotype. GSM. 92926a, b (figured Whittard 1958, pl. 15, figs. 6–8).
Paratypes. Wattison Collection W 3; GSM. 92927; GSM. 92928; GSM. 92929 (figured Whittard 1958, pl. 15, figs. 9, 11, 10, 12, 13 respectively).

Type localities and horizons. All the type material is from the shales interbedded in the Stapelely Volcanic Group, Lower Llanvirn of Nind Quarry, Shropshire, with the exception of GSM 92929 which is from the topmost Hope Shales, Lower Llanvirn, in the path west of Brithdir, near Old Church Stoke, Shropshire.

Discussion. In his redescription of *P. sedgwickii* from Shropshire, Whittard (1958 : 113–115) considered that the slight differences between the holotype from Builth and the Shropshire material to be unimportant systematically. However, the absence of sunken granules from the thoracic and pygidial surfaces and the broader, more spatulate terminations of the third pygidial pleurae, are sufficiently consistent to warrant the subspecific separation of the Builth and Shelve forms.

Family **CALYMENIDAE** Burmeister 1843
Genus ***FLEXICALYMENE*** Shirley 1936

Diagnosis. Glabella outline generally subparabolic; anterior border moderately long (*sag.*) and usually inclined forwards; eyes generally approximately opposite 2p lobes. Thorax generally with 13 segments.

Type species. *Flexicalymene caractaci* (Salter).

Distribution. The genus ranges from the Lower Llanvirn to the Ashgill (Zone 4, Ingham 1966) and is widely distributed throughout the British Isles, Bohemia and eastern North America. Its Llanvirn occurrences are limited to the Anglo-Welsh region.

Discussion. Prior to this study the genus was not known from rocks older than the Upper Llanvirn. However, a new calymenid recovered from the Llanvirn of the Builth region is best assigned to *Flexicalymene*. The inclusion of this new species within *Flexicalymene* enlarges the concept of the genus to embrace stocks with a glabella which is rather more square anteriorly than is typical.

Flexicalymene aurora sp. nov.

(Pl. 8, fig. 7; Pl. 9, figs. 1, 2, 4, 7, 8)

1940 *Calymene* (*Flexicalymene*) *aldonensis* Reed; Elles : 396, 398, 432.

Diagnosis. *Flexicalymene* with trapezoidal glabella with four pairs of lateral glabellar lobes with rounded outlines; mid-point of eyes opposite second pair. Pygidial axis broad with six axial rings and terminal piece; pleural fields with four ribs.

Type material. Holotype. It. 2974 (Pl. 9, fig. 4). Internal mould of nearly complete cephalon and anterior five thoracic segments.

Paratypes. It. 2975 (Pl. 8, fig. 7). Internal mould of damaged cranidium. It. 2976 (Pl. 9, figs. 1, 2). Internal and external moulds of left librigena. It. 2977 (Pl. 9, fig. 7). Internal and external moulds of pygidium. It. 2978 (Pl. 9, fig. 8). Internal and external moulds of pygidium.

Dimensions.

	A	B	B_1	B_2	B_3	B_4	C
Holotype . .	8·5	6·5	5·2	3·5	2·2	1·2	3·3
It. 2975 . .	—	5·1	4·2	2·9	1·8	0·9	2·8

	I	J_1	K	K_1
Holotype . .	17·5	10·7	3·3	5·9
It. 2975 . .	—	—	—	4·7

	W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	Right
It. 2977 . .	11·5	4·6	2·5	6·4	6·9	6	4	4
It. 2978 . .	9·2	3·0	—	—	4·8	5+	4	4

All measurements in mm. For explanation of symbols see Text-fig. 4.

Type localities and horizon. The holotype and paratypes, with the exception of It. 2978, are from the exposures on the north side of the track leading from Bwlch-llŵyn to Hendy Bank, 100 yards east of Bwlch-llyn. Paratype It. 2978 is from the cliff section in the left bank of the Howey Brook half a mile east-south-east of Carregwiber. Both localities lie in the *Didymograptus speciosus* Subzone of the Lower Llanvirn.

Distribution. This new species is known only from the two localities cited above.

Description. No entire specimens are known, but it is estimated that the total length would be about two and a half times the maximum width occurring along the posterior cephalic margin.

The semicircular cephalon is about twice as wide as long; the glabella occupies about one-quarter of the posterior width, tapering anteriorly to about one-half of its posterior width across the frontal lobe. The glabellar length is slightly greater than its anterior width. Four pairs of rounded, clearly defined lateral glabellar lobes are developed, *1*p being the largest and of oval outline. *1*p furrows are deep and bifurcate axially, the major branch turning posteriorly towards the occipital furrow which it fails to reach; the other branch is short and notches the posterior of the *2*p lobes. These are nearly circular in outline, about half the size of the *1*p pair, and are constricted at their base anteriorly by the *2*p furrows and posteriorly by the anterior branch of the *1*p furrows. The *2*p furrows are deep and similar to *1*p, with the exception that no anterior branch is developed axially. The *3*p lobes are smaller, wider (*tr.*) than long (*exsag.*), and anteriorly defined by short, more or less transversely directed *3*p furrows. The *4*p lobes are very small, similar in outline to the *3*p, though shorter (*exsag.*) and defined anteriorly by little more than tiny notches forming the *4*p furrows. The axial furrows are deep and slightly constricted opposite the *3*p lobes by a small buttress formed by an extension of the weak eye ridges (Pl. 9, fig. 4). The occipital ring is typically calymenid with the occipital furrow deflected round the posterior of the *1*p lobes. No median occipital node appears to be developed. The preglabellar field is not known.

The genal regions are moderately convex and extend very slightly anterior to the glabella. The mid-point of the eyes is situated approximately in line (*tr.*) with the centre of the *2*p lobes and about half-way across the genae. The posterior border furrow is well developed, straight and in common with the border, becomes wider laterally. The librigenae are typically calymenid in form with well-developed convex border and border furrow. The rostral plate is axe-shaped and underlies virtually the whole of the preglabellar field (Pl. 9, fig. 4).

The total number of thoracic segments is unknown but at least five are present; their form is typically calymenid.

The pygidium is rather like a taut bow in outline, being slightly less than twice as wide as long. The axis is relatively wide, anteriorly about one-third of the pygidial width, tapering posteriorly to about one-half this width. Six axial rings and a terminal piece are present in paratype It. 2977 but possibly only five in It. 2978. The pleural fields possess four furrowed ribs with a relatively large terminal area. The rib furrows are most pronounced laterally. The external surface is ornamented with small tubercles, which appear to be larger and more closely spaced in the marginal regions.

Discussion. This, the earliest known *Flexicalymene*, is similar to many of the later species, such as *F. cambrensis* (Salter 1865), *F. caractaci* (Salter 1865), *F. acantha* Bancroft 1949 and *F. cobboldi* Dean 1963. However it differs from all of these in the rather square anterior of the glabella. The new species is about the same age as *Platycalymene tasgarensis* Shirley 1936 from the Hope Shales of the Shelve region, although *F. aurora* is easily distinguished by the more rounded outlines of its lateral glabellar lobes, particularly the *2*p lobes, and by the development of small buttresses opposite the *3*p furrows. The glabella also appears to be relatively longer and the eyes more posteriorly placed in *F. aurora* but the significance of this is difficult to assess until a larger sample is known.

Genus *PLATYCALYMENE* Shirley 1936

Diagnosis. Calymenid like *Flexicalymene* but depressed and with anterior border more roll-like; eyes opposite second or third lateral glabellar lobes. Lateral glabellar lobes rather rectangular, not rounded; anterior of glabellar rather square.

Type species. *Platycalymene duplicata* (Salter).

Distribution. The genus is now known from the Lower Llanvirn, Llandeilo and Basal Caradoc of the Welsh Borderland and also from the Tramore Limestone in County Waterford. It has also been recorded from the *Chasmops* Limestone of Skåne in beds approximately equivalent to the *Dicranograptus clingani* Zone.

Discussion. Since Shirley's sub-division of the calymenids there has been discussion as to the validity of some of his genera. However, with the exception of Richter (1940), most workers have accepted his basic divisions, although *Reacalymene* is generally taken as a subgenus of *Flexicalymene* (see Dean 1962 : 112). The only addition to the Ordovician genera has been the introduction of *Onnicalymene* Dean 1962 for those forms previously attributed to *Flexicalymene* in which the palpebral lobes are opposite the *1*p lobes.

Shirley (1936 : 395) defined *Platycalymene* as a depressed form with parabolic outline to the glabella with three pairs of lateral glabellar lobes, and a short pre-gabellar field with a roll-like anterior border. At present four species are generally referred to this genus, namely the types species *P. duplicata* (Salter 1865) from the Basal Caradoc of the Welsh Borderland, *P. tasgarensis* Shirley 1936 from the Lower Llanvirn of Shropshire, *P. eire* Lamont 1949 from the Tramore Limestone of County Waterford, and *P. dilatata* (Tullberg 1882) from the *Chasmops* Limestone of Skåne. Of these, neither *P. eire* nor *P. dilatata* are well known; both may be junior synonyms of *P. duplicata*, as the only differences appear to be slight variations in glabellar proportions. Cephalic profiles of both *P. duplicata* and *P. tasgarensis* show that the anterior border is not so pronounced as Shirley indicated (1936 : 391), but is more steeply inclined and more convex than is typically found in *Flexicalymene*. This difference alone seems insufficient to distinguish between the two genera. The position of the palpebral lobes is of little use in distinguishing *Platycalymene*; they may be opposite the *3*p lobes as in the type species or opposite the *2*p as in *P. tasgarensis*, a condition typical of most *Flexicalymene*. However, there is a further difference which was not stressed by Shirley, involving the outline of the lateral glabellar lobes. In *Flexicalymene* the glabella is typically subparabolic in outline with well-rounded lateral glabellar lobes. In *Platycalymene* the glabella is better described as trapezoidal and the lateral glabellar lobes are more rectangular in outline (compare *F. aurora*, Pl. 8, fig. 7 with *P. duplicata*, Pl. 10, fig. 5). This difference, together with that of the cephalic profiles, is considered sufficient to warrant the continued separation of *Platycalymene* from *Flexicalymene*, although a full revision of the Ordovician calymenids might not uphold this. It is interesting to note that, for the Anglo-Welsh region at least, *Platycalymene* is restricted to shaly facies and *Flexicalymene* is generally confined to the more calcarenitic facies, and it may subsequently be found that *Platycalymene* is simply a facies variant of *Flexicalymene*.

Platycalymene duplicata (Murchison)

(Pl. 9, figs. 5, 6; Pl. 10, figs. 1–8; Pl. 11, figs. 1–9; Pl. 12, figs. 1, 4, 5)

1839 *Asaphus duplicatus* Murchison : 661–662, pl. 25, fig. 8.
1852 *Calymene duplicata* (Murchison); Barrande : 574.
1927 *Calymene* (*Metacalymene*) *duplicata* (Murchison); Kegel : 619.

1936 *Platycalymene duplicata* (Murchison); Shirley : 390–395, 399, 400, 403.
1940 *Calymene* (*Metacalymene*) *duplicata* (Murchison); Richter : 1031.
1960 *Platycalymene duplicata* (Murchison); Whittard : 151, 154–157, pl. 21, figs. 13–15. Includes full synonymy.
1960 *Platycalymene duplicata* (Murchison) *parallela* Whittard : 157, pl. 21, fig. 16.
1966 *Platycalymene duplicata* (Murchison); Whittard : 300.
1966 *Platycalymene duplicata* (Murchison) *parallela* Whittard; Whittard : 300.

Diagnosis. *Platycalymene* with three, occasionally four lateral glabellar lobes; mid-point of eyes opposite *3*p furrows. Pygidium semi-oval generally with nine axial rings and terminal piece and eight ribs. Entire exoskeleton rather depressed.

Holotype. GSM. 6847 (Pl. 9, fig. 6). Internal mould of pygidium and associated external mould of thorax.

Dimensions.

W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
16·0	3·6	1·8	6·9	7·7	9	9 + i	9 + i

All measurements in mm. For explanation of symbols see Text-fig. 4. The suffix +i indicates the development of a further incipient rib.

Type locality and horizon. The label affixed to the holotype records it as being from the "uppermost trilobite bed, Wilmington, near Marton Pool". Whittard (1960 : 156) however has pointed out that Wilmington is located on the Aldress Shales from which no calymenids are recorded. He concludes from the known occurrences of the species in the Shelve district and also on lithological grounds that the holotype may be either from the Rorrington Beds or the Spy Wood Grit.

Other figured material. It. 2982 (Pl. 11, fig. 9); It. 2983 (Pl. 10, fig. 8); It. 2984 (Pl. 11, fig. 5); It. 2985 (Pl. 11, fig. 7); It. 2986 (Pl. 12, fig. 5); It. 2988 (Pl. 10, fig. 4); It. 2989 (Pl. 10, fig. 7); It. 2990 (Pl. 11, fig. 6); It. 2991 (Pl. 11, fig. 8); It. 2994 (Pl. 12, fig. 1); It. 2995 (Pl. 11, fig. 4); It. 3000 (Pl. 10, fig. 3); It. 3001 (Pl. 11, fig. 2); It. 3002 (Pl. 10, fig. 2); It. 3003 (Pl. 10, fig. 1); It. 3006 (Pl. 11, fig. 3); It. 3007 (Pl. 11, fig. 1, Pl. 12, fig. 4); It. 3008 (Pl. 10, fig. 6); It. 3009 (Pl. 9, fig. 5); Wattison Coll. H. 13 (Pl. 10, fig. 5).

Distribution. The species is recorded only from the Shelve and Builth regions. In the Shelve region Whittard (1960 : 156) records it from high in the *Nemagraptus gracilis* Zone to probably low in the *Diplograptus multidens* Zone. In the Builth region it occurs throughout beds of the *N. gracilis* Zone, the only Caradocian rocks exposed in the Builth area.

Description. The maximum width of entire exoskeleton is about two-thirds of the total length and is attained across the posterior of the cephalon. Posterior to this the exoskeleton tapers gently, being only about one-half of the total length across the anterior of the pygidium. The general transverse convexity of the exoskeleton is low, although the axis is moderately convex and the lateral portions, particularly of the thorax are deflected ventrally. Small tubercles of varying size, up to 0·15 mm. in diameter, are developed over the entire dorsal surface. The larger ones, though present over all parts, show concentrations along the anterior and lateral margins (Pl. 10, fig. 4; Pl. 11, fig. 5).

The cephalon is between two and a half and three times as wide as long, with rounded margins laterally which become straight anteriorly. The trapezoidal glabella, with posterior width about equal to length, occupies about one-quarter of

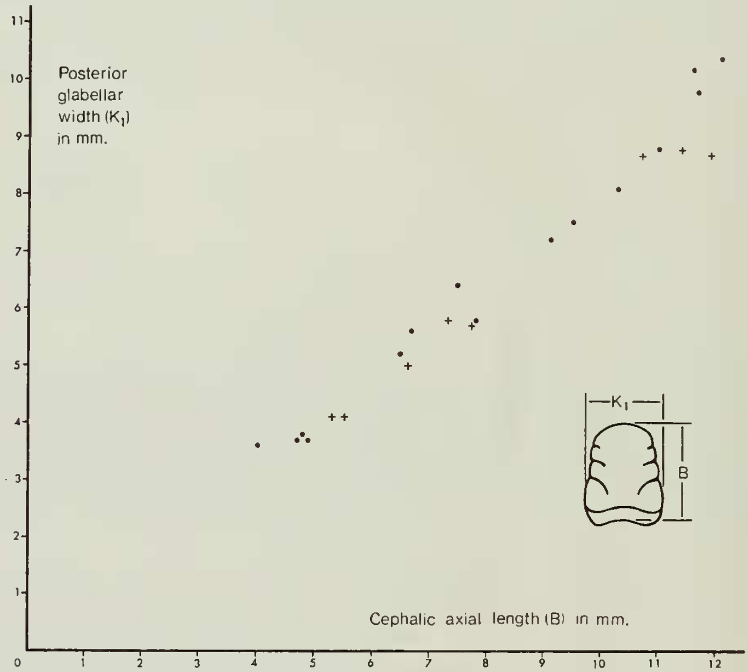

Fig. 5. Graph of cephalic axial length (B) against posterior glabellar width (K_1) of *Platycalymene duplicata* (Murchison) illustrating the lack of " wide " and " narrow " forms. • = specimens from the middle quarry, Llanfawr, Llandrindod; + = specimens from the quarry at Gwern-yfed-fâch half a mile south-east of Builth Road station.

the posterior cephalic width and tapers gently to the anterior. Some variation in the glabella proportions is present, but the existence of distinct " wide " and " narrow " forms cannot be demonstrated (see Text-fig. 5). The variation in the glabellar proportions may or may not have been accentuated by *post-mortem* deformation; it is believed that the glabellar outline of *P. duplicata parallela* Whittard is a result of such deformation and is thus included here in the synonymy. Although convex both sagittally and transversely, the sagittal convexity of the glabella is much less than in most other calymenids. Cephalic profiles obtained from internal moulds of the Builth material (Text-fig. 6) do not show such a pronounced roll-like anterior border as figured by Shirley (1936 : 391), but they show a more convex border than is typical of *Flexicalymene*. Whilst it is conceded that the Builth material may be slightly flattened, profiles from material from the Spy Wood Grit of the Shelve region also fail to show such a pronounced roll-like border.

Three pairs of lateral glabellar furrows are developed, but occasionally traces of a fourth pair are present (Pl. 11, fig. 9). Also in some specimens only the *1*p and *2*p furrows are developed (Pl. 11, fig. 6). The *1*p furrows are the most strongly developed, extending from about one-third the way along the glabella and being curved posteromedianly, just failing to reach the occipital furrow. The slight outward convexity of the axial furrows together with the *1*p furrows impart an outline to the *1*p lobes similar to a cat's ear. The *2*p furrows situated slightly more than half-way along the glabella are shorter, directed posteromedianly and only slightly curved, giving a parallel-sided outline to the *2*p lobes. The *3*p furrows are situated between about three-quarters and four-fifths the way along the glabella and are generally rather weakly developed forming shallow, straight posteromedianly directed depressions on the flanks of the glabella (Pl. 10, fig. 5; Pl. 12, fig. 5). When *4*p furrows are developed they take the form of very shallow, short, transversely directed furrows (Pl. 11, fig. 9). The simple occipital ring is bounded by a clearly incised occipital furrow which is deflected laterally round the posterior of the *1*p lobes. About four-fifths of all internal moulds show indications of a small, though distinct, median occipital node, which is apparently absent on the remaining one-fifth. Evitt & Whittington (1953) showed that the wing process on the anterior wings of the hypostoma indents the anterior apodemes at the point of their contact. This also appears to be the case in *P. duplicata*, for the indentations, occurring as tiny spike-like structures in the anterior fossulae of internal moulds, are clearly present (Pl. 12, fig. 1). Lamont (1949 : 314; 1950 : 300) has recorded the presence of a second pair of fossulae in *P. duplicata* slightly to the posterior. These are present directly behind the eye ridge on the fixigenae (Pl. 11, fig. 9), and it is thought that Stubblefield's (1950 : 67) suggestion that they are a complimentary structure to the eye ridge is preferable to the idea that they indicate a tripart origin of the frontal lobe (Lamont 1949 : 314).

The gently convex genal regions extend slightly anterior to the glabella. The posterior border furrow is deep and straight. The posterior border is narrow axially expanding laterally to about four times its initial width. Small palpebral lobes are situated with their mid-point opposite the *3*p furrow and just over one-third the way across the genae. The visual surface of the eye is not known. A weak eye ridge extends from the palpebral lobe to the axial furrows (Pl. 10, fig. 5). The anterior branch of the facial suture is directed more or less exsagittally from the eye, curving axially towards the anterior border. The posterior branch is directed approximately transversely from the eye before curving posteriorly to cut the genal angle (Pl. 10, fig. 3). The librigenae possess a prominent convex border and a well developed border furrow (Pl. 10, fig. 4). The larger dorsal tubercles (diameter ranging from 0·10–0·15 mm.) are perforated near their summit, the pores being about 0·03 mm. in diameter. No evidence has been found of openings on the slopes of the tubercles (see Evitt & Whittington 1953 : 53). The ornamentation is absent in the lateral glabellar furrows (Pl. 11, fig. 1). Whittard (1960 : 148) described a similar feature in

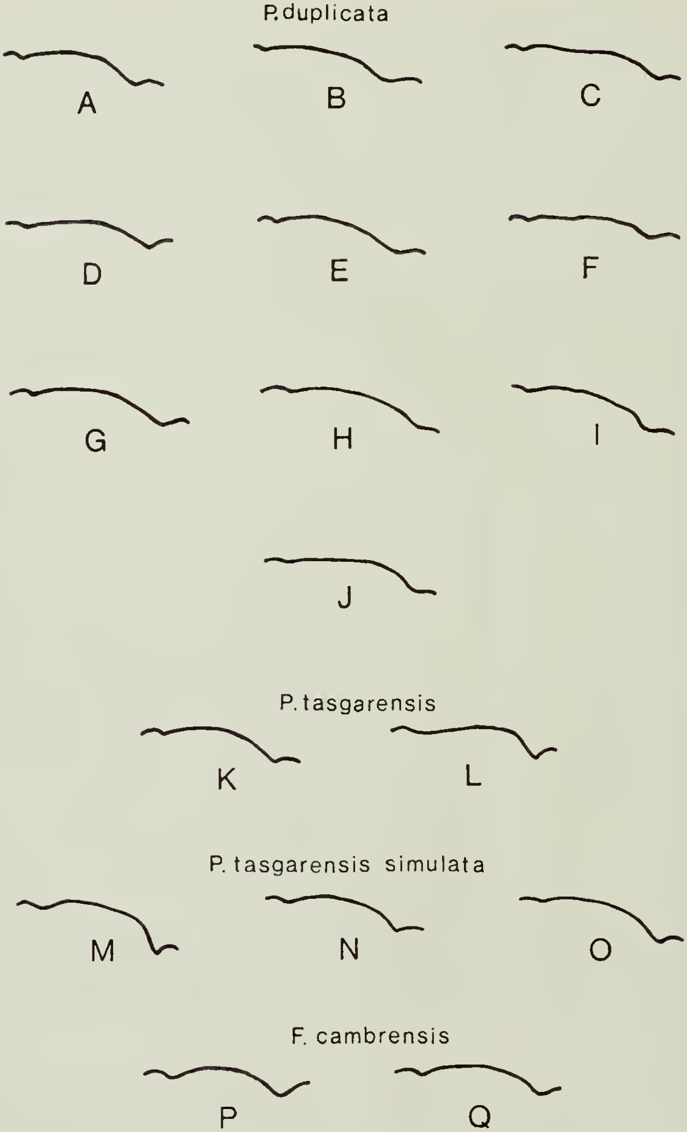

FIG. 6. Diagram showing the similarity of cephalic profiles of *Platycalymene duplicata* (Murchison), *P. tasgarensis* Shirley, *P. tasgarensis* Shirley *simulata* subsp. nov., and *Flexicalymene cambrensis* (Salter). All profiles drawn to a standard length. (A. It. 2990, B. It. 2993, C. It. 2997, D. It. 2995, E. It. 2981, F. It. 2996, G. It. 2987, H. GSM 87127, I. GSM. 87126, J. GSM. 87130, K. GSM. 87119, L. GSM. 87120, M. It. 3014, N. It. 3015, O. It. 3013, P. It. 2980, Q. It. 2979). A–G from the middle quarry, Llanfawr, Llandrindod; H, I, J from the Spy Wood Grit, Rorrington, Shropshire; K, L from the Hope Shales, Whitsburn Dingle, Shropshire, M, N from the stream section south-east of Tre coed; O from the Dulas Brook; P, Q from the east end of the Pheasantry, Dynevor Park, Llandeilo.

P. tasgarensis which he considered corresponded with muscle attachment areas on the internal surface; these areas in *P. duplicata* appear to be of a similar nature.

The subrectangular hypostoma has gently concave lateral margins with a total length of about one and a third times the maximum width. The median body is strongly convex ventrally and divided by a shallow furrow into an oval anterior lobe about three and a half times as long as the crescentic posterior lobe. Conspicuous oval maculae are present in the posterolateral regions of the anterior lobe. In some specimens the furrows bounding the anterior of the maculae are continuous medianly, though very shallow, and together with the furrow bounding the posterior of the anterior lobe give the impression of a slight ridge crossing the median body with the maculae situated at the lateral ends. The anterior border is long (*sag.*) and flexed sharply ventrally at about half-way between the anterior furrow and the margin. Well-developed anterior wings have a deep pit ventrally near the anterolateral extremity, with a corresponding boss dorsally. The lateral border furrows shallow towards the anterior and posterior, the associated borders being narrow and flexed ventrally. The posterior border is flat, forked, with the median notch extending forwards nearly to the well developed posterior border furrow. The ventral surface of the lateral and posterior borders and border furrows is ornamented with small tubercles (Pl. 10, fig. 8).

The thorax consists of 13 segments. The axial rings are transversely convex, simple, and with weak lateral nodes. The articulating furrow is well developed, deepening laterally to form deep apodemal pits. The fulcrum of the anterior segments is situated more distally than in the posterior segments and it appears that in general the posterior pleurae are more steeply deflected ventrally than the anterior ones, thus the thorax becomes slightly narrower and more convex posteriorly (Pl. 10, fig. 6). The pleural furrows are well developed axially, becoming shallower beyond the fulcrum.

The semi-oval pygidium is rather compressed anteriorly, and about twice as wide as long. The axis is well defined, transversely convex and anteriorly occupies about one-quarter of the pygidial width. It tapers posteriorly to about half its anterior width, the greater part of the tapering occurring over the anterior half of the axis. Nine axial rings are generally developed but some specimens have eight or ten (see Table 26). No evidence has been found to support Whittard's claim (1960 : 155) that where fewer rings are developed, the terminal piece is proportionately longer. The ring furrows of the anterior five or six rings deepen laterally to form apodemal pits. The pleural fields possess eight normally well-developed ribs, although nine may be present (see Table 27). The ribs have a median furrow typically present only on the distal half, but in a few specimens (Pl. 10, fig. 2) it may be traced along the entire rib length. In nearly all specimens a notch near the posterior of each rib, at its axial end, corresponds to the axial end of the furrow. Only one known pygidium shows irregularities in rib development; this is thought to have been the result of injury (Pl. 11, fig. 2).

ONTOGENY. A single tiny glabella (Pl. 11, fig. 3), 1·6 mm. long is believed to be a meraspis, degree unknown. Although basically similar to adult glabellae, it shows some minor differences. Posteriorly it is about as wide as long, but tapers slightly anteriorly. The anterior margin is slightly more rounded than is generally the case in holaspides. Three pairs of lateral glabellar furrows are developed. *1*p are prominent and frontally of similar form to those of the adult; posteriorly they extend to cut the occipital furrow, thus isolating the *1*p lobes. The short *2*p furrows are directed posteromedianly as in adult specimens. The *3*p furrows are only weakly developed, being little more than a prominent notch in the sides of the glabella. Although the occipital ring is not preserved it is evident that the occipital furrow is of the same form as in the holaspides, being deflected posteriorly round the *1*p lobes. Some form of preglabellar field is present, but details are not preserved.

Dimensions

B_1	B_2	B_3	B_4	K	K_1
1·6	1·1	0·7	0·3	1·2	1·7

All measurements in mm. For explanation of symbols see Text-fig. 4.

Biometrical data. Much data is available for this species from both the Middle quarry, Llanfawr, and the quarry at Gwern-yfed-fâch. However, comparison of the bivariate statistics and pygidial data shows there are no significant differences between the two samples. The data given below are based on the larger sample obtained from the former locality.

Table 23

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : B_1	8·23	6·7656	6·89	4·8411	0·997	0·996	1·01	0·0005	0·85	0·00025	19
B : B_2	8·23	6·7656	4·53	2·0000	0·988	0·988	0·99	0·0014	0·54	0·00042	19
B : B_3	8·15	7·0300	2·82	0·8935	0·991	0·991	1·03	0·0012	0·36	0·00014	18
B : B_4	8·35	6·6812	1·84	0·3950	0·973	0·974	1·10	0·0041	0·24	0·00021	17

Bivariate statistics for the glabella of *P. duplicata* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

Table 24

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : C	8·00	7·2600	5·65	3·8075	0·993	0·993	1·02	0·0013	0·72	0·00067	13
B : K_1	8·15	7·9900	6·65	5·9400	0·990	0·990	1·05	0·0017	0·86	0·00114	15
K_1 : K	6·84	5·9550	4·91	2·8105	0·984	0·985	0·96	0·0013	0·69	0·00071	23
A : B	10·62	8·9993	8·70	6·3240	0·994	0·994	1·02	0·0009	0·84	0·00060	16

Bivariate statistics for the cephalon of *P. duplicata* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

Discussion. As already mentioned *P. eire* and *P. dilatata* may be synonyms of *P. duplicata*. *P. eire*, from the Tramore Limestone of County Waterford, supposedly has a slightly more convergent glabella than is typical of *P. duplicata*, but examples similar to *P. eire* are known from Builth (compare Lamont 1949, pl. 18, fig. 1 with Pl. 11, fig. 6). *P. dilatata* from the *Chasmops* Limestone of Skåne is not well known

TABLE 25

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	20·20	94·9200	10·26	25·3325	0·996	0·997	1·02	0·0021	0·52	0·00071	5
W : X	22·84	88·5929	5·34	5·6133	0·993	0·994	1·07	0·0027	0·25	0·00018	7
Y : X	10·20	13·4512	5·13	4·0725	0·984	0·986	1·09	0·0022	0·55	0·00064	17
X : X_1	5·10	3·8482	2·48	0·7665	0·981	0·982	0·92	0·0019	0·45	0·00047	18
Z : Y	10·85	15·2747	9·74	12·0188	0·995	0·996	0·99	0·0005	0·89	0·00049	18

Bivariate statistics for pygidium of *P. duplicata* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 26

	Number of axial rings		
	8	9	10
Number of specimens . .	2	12	3

mean = 9·06; var. = 0·5763; n = 17

Frequency distribution of the number of axial rings developed on internal moulds of *P. duplicata* (Murchison), together with the means and variance.

2 × 2 probability tests show that there is no correlation between either the number of axial rings or the number of pleural ribs developed and the size of the pygidium as measured by the pygidial length.

TABLE 27

Number of ribs . . .	7 + i	8	8 + i	9
Number of specimens . .	1	14	3	5

mean = 8·26; var. = 0·2024; n = 23

Frequency distribution of the number of ribs developed on internal moulds of *P. duplicata* (Murchison) together with the mean and variance. The suffix " +i " indicates the development of a further incipient rib. Such a rib was counted as half a rib for the purposes of calculating the mean.

TABLE 28

mean = 8·0; var. = 0·0454; n = 12

Mean and variance for the number of ribs developed on external moulds of pygidia of *P. duplicata* (Murchison).

Comparison of these data with those for internal moulds (Table 27) shows no significant difference.

but apparently has no furrows developed on the pygidial ribs. No definite decision as to the validity of this species can be made until it is redescribed. It is considered that the different glabellar outline of *P. duplicata parallela* Whittard is due to compression and that it should not be separated from *P. duplicata s.s.*

P. tasgarensis Shirley 1936 is easily distinguished by its more posteriorly placed eyes and also the wider pygidial axis with fewer axial rings and only four ribs. *P.* cf. *duplicata* (below) from the uppermost Llandeilo of the Builth region is similar to *P. duplicata* and may be distinguished only by the fewer ribs on the pleural fields.

Although it has been shown (Text-fig. 5) that distinct "wide" and "narrow" forms are not present, two forms of cephala are distinguishable, those with, and those without a median occipital node. It has been suggested that the presence or absence of occipital structures, generally occipital spines, in forms otherwise alike may indicate male and female forms, the males lacking the spine (Hu 1963; Bell & Ellinwood 1962; Lochman & Hu 1959). If this is so, the males of *P. duplicata* would be in a minority of about one to four. In this respect it is perhaps worth noting that modern arthropod populations commonly have a considerably higher proportion of females than males.

Platycalymene cf. ***duplicata*** (Murchison)

(Pl. 12, figs. 2, 7)

1940 *Platycalymene duplicata* (Murchison); Elles : *pars.* 411, 417, 432.

Figured material. It. 3011 (Pl. 12, fig. 7). Internal mould of cranidium. It. 3012 (Pl. 12, fig. 2). Internal mould of pygidium.

Dimensions.

	A	B	B_1	B_2	B_3	B_4	C
It. 3011	3·6	3·0	2·5	1·6	1·1	0·7	1·4

	I	J	K	K_1
It. 3011 . .	8·5	2·8	1·6	2·2

	W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
It. 3012	6·7	1·8	0·8	3·2	0·6	8	6	6

All measurements in mm. For explanation of symbols see Text-fig. 4.

Locality and horizon. Small quarry at the south-western end of Pen-cerig Lake, in shales of uppermost Llandeilo age.

Discussion. The cranidium and pygidium differ in some respects from those of *P. duplicata* from the overlying Basal Caradoc. The cranidium, which is small, has a more convex cephalic profile; the pygidium, which again is rather small compared with the majority of specimens of *P. duplicata*, possesses only six ribs, plus an obscure seventh, on the pleural fields; that is fewer than in any specimen known from the Basal Caradoc. The close relationship between this form and *P. duplicata* cannot be denied and yet the pygidium shows some affinity to *Platycalymene tasgarensis simulata* subsp. nov. (p. 93) occurring lower in the Llandeilo of the Builth region, with its fewer number of pleural ribs and more bow-like outline. However, the pygidium differs from *P. tasgarensis simulata* in its more slender axis and slightly higher number of axial rings.

Platycalymene tasgarensis Shirley ***simulata*** subsp. nov.

(Pl. 12, figs. 3, 6, 8–10; Pl. 13, figs. 1–3)

1940 *Platycalymene duplicata* (Murchison); Elles : *pars*. 411, 412, 432.

DIAGNOSIS. *Platycalymene* with relatively high convexity, three pairs of rather angular lateral glabellar lobes and squarish glabellar anterior; mid-point of palpebral lobes opposite 2p furrows. Pygidium with seven axial rings and six well-developed pleural ribs.

TYPE MATERIAL. Holotype. It. 3013 (Pl. 13, fig. 3). Internal mould of cranidium.

Paratypes. It. 3014 (Pl. 12, fig. 3). Internal and external moulds of cranidium. It. 3015 (Pl. 12, fig. 10; Pl. 13, fig. 2). Internal and external moulds of cranidium. It. 3016 (Pl. 12, figs. 8, 9). Internal and external moulds of pygidium. It. 3017 (Pl. 13, fig. 1). Internal and external moulds of pygidium. It. 3018. Internal mould of pygidium.

DIMENSIONS.

	A	B	B_1	B_2	B_3	B_4	C
Holotype	8·3	6·8	5·6	3·6	2·2	1·4	3·2
It. 3014	4·3	3·6	3·0	2·0	1·3	0·8	—
It. 3015	5·7	4·8	3·9	2·5	1·7	1·1	2·5

	I	J	J_1	K	K_1
Holotype . .	17·0	6·9	9·5	3·6	6·3
It. 3014 . .	10·3	—	—	2·3	3·2
It. 3015 . .	—	—	—	2·6	3·6

	W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
It. 3016	*c.* 13·5	4·3	1·8	5·6	6·5	7	6	6
It. 3017	*c.* 9·0	3·1	1·5	4·0	4·6	6	6	6
It. 3018	13·0	3·9	1·9	6·0	6·9	7	6	6

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITIES AND HORIZONS. The holotype is from Llandeilo shales outcropping in the left bank of the Dulas Brook, 150 yards south-west of the old quarry 350 yards west of Maesgwynne, and 60 yards north of spot height 727. Paratypes It. 3016, It. 3017 are from the stream section 15 yards south-west of the above quarry, the remaining paratypes being from the stream section south-east of Tre coed, It. 3014 from the easterly end, 160 yards south-east of the farm and It. 3015, It. 3018 from the westerly end 120 yards from the farm.

OTHER FIGURED SPECIMEN. It. 3019 (Pl. 12, fig. 6).

DISTRIBUTION. The species is rare in the Builth region where it is recorded only from the localities yielding the type material.

Description. The dimensions of the complete exoskeleton are not known. The cephalon is slightly over twice as wide as long and is roughly semicircular in outline, but rather straight anteromedianly. The glabella is convex both transversely and longitudinally. In outline it is trapezoidal and may vary from being slightly wider than long to slightly longer than wide. Three pairs of lateral glabellar furrows are developed. *1*p are the strongest and are angulated at about their mid-length, the anterior portion being directed posteromedianly at about 30° to the transverse direction and the posterior portion becoming nearly parallel to the sagittal direction, extending towards, but not reaching, the occipital furrow. The *2*p furrows are shorter, and for the greater part parallel to the anterior portion of the first pair, but axially they curve slightly to the posterior. These two pairs of furrows define rather square *2*p lobes. The *3*p furrows are even shorter and are more weakly developed, but again are parallel to the outer portions of the first two pairs. Specimen It. 3015 shows indications of a fourth pair of furrows which form little more than a notch in the glabellar sides opposite the weakly developed buttress at the end of the eye ridge (Pl. 12, fig. 10). The occipital ring is simple with a small median node generally present, though this is apparently not developed in the holotype (Pl. 13, fig. 3). The occipital furrow is well incised and laterally is deflected round the posterior of the *1*p lobes. Although the cephalic profile does not match well with that given by Shirley for the type species of *Platycalymene*, the anterior border is more steeply inclined and roll-like than is typical of *Flexicalymene* (Text-fig. 6).

The genal regions are moderately convex, and extend slightly in front of the glabella. The mid-point of the palpebral lobes is about opposite the *2*p furrows, and situated about one-third of the way across the genae. Weakly developed eye ridges (Pl. 12, fig. 10) reach the axial furrows just anterior of the *3*p furrows. The posterior border and border furrows are well developed, expanding distally and also curving gently to the anterior. The librigenae are typically calymenid with prominent border and border furrows (Pl. 12, fig. 6).

Virtually all the external surface of both cephalon and pygidium is covered with small tubercles, some slightly larger than others. However, as in many other calymenids the slopes of the lateral glabellar furrows lack tubercles and are thought to correspond to areas of muscle attachment on the internal surface of the exoskeleton (Pl. 13, fig. 2).

The thorax is not known.

The pygidium has a " taut bow " outline and is generally slightly less than twice as wide as long. The axis is relatively wide anteriorly occupying nearly one-third of the pygidial width. It tapers more or less uniformly posteriorly and possesses seven transversely convex axial rings together with a terminal piece. The pleural fields possess six well-developed ribs which are furrowed more or less along their entire length (*tr.*), the furrows becoming shallower medianly.

Discussion. This new subspecies from the Llandeilo is similar to *P. tasgarensis* from the Lower Llanvirn of the Shelve region. The only differences appear to be in the straighter cephalic axial furrows, and the slightly higher number of pygidial ribs developed in the Builth specimens. The new subspecies is readily distinguished from *P. duplicata* by its more posteriorly placed eyes and lower number of axial rings and pleural ribs developed on the pygidium. The same criteria serve to distinguish *P.* cf. *duplicata*.

Family **COLPOCORYPHIDAE** Hupé 1953

Genus ***PLAESIACOMIA*** Hawle & Corda 1847

TYPE SPECIES. *Plaesiacomia rara* Hawle & Corda.

DISTRIBUTION. Lower Llanvirn of Wales, Caradoc and possibly Llandeilo of France, Spain, Portugal, Bohemia and North Africa.

DISCUSSION. Dean (1966*a*) has recently reviewed *Plaesiacomia* together with *Colpocoryphe* Novak *in* Perner 1918 and concluded that the two genera should not be considered as synonymous as was suggested by Vaněk (1965). If the specimens from Builth described below are correctly assigned, they are of particular interest not only as the first record of this typically Mediterranean genus in Britain, but it is by far the earliest known occurrence so far recorded.

Plaesiacomia sp.

(Pl. 13, figs. 4–8; Pl. 14, figs. 1–2)

FIGURED MATERIAL. It. 3023 (Pl. 14, fig. 2). Internal mould of damaged cranidium. It. 3024 (Pl. 13, figs. 7, 8). Internal mould of damaged cranidium. It. 3025 (Pl. 14, fig. 1). External mould of damaged cranidium. It. 3026 (Pl. 13, figs. 4, 5). Internal mould of pygidium. It. 3027 (Pl. 13, fig. 6). Internal mould of pygidium.

DIMENSIONS.

	B	K		W	X	Z
It. 3023	5·0	*c.* 4·7	It. 3026	*c.* 5·5	*c.* 2·6	*c.* 3·8
It. 3024	3·9	3·6	It. 3027	*c.* 4·2	*c.* 2·0	*c.* 2·7

All measurements in mm. Where B is the sagittal glabellar length including the occipital ring; K the maximum glabellar width; W the maximum pygidial width; X the anterior pygidial axial width; Z the sagittal pygidial length.

LOCALITY AND HORIZON. Exposures on the left bank in the ravine in the upper reaches of the Camnant Brook immediately north of the prominent " S " bend 230 yards S. 13° W. of the fence crossing near the stream source in beds of Lower Llanvirn age.

DESCRIPTION. The glabella is smooth, gently convex and tapers towards the anterior. The occipital ring is narrow, but clearly differentiated from the glabella by the occipital furrow. The axial furrows and preglabellar furrow are deep and fairly steep-sided. Anteriorly a narrow border is developed (Pl. 13, figs. 7, 8), but shows little transverse convexity and only a slight notch is developed. The palpebral lobes appear to have been relatively small and situated about two-thirds the way along the glabella from the posterior. The fixigenae are gently convex, wide posteriorly with the facial sutures presumably cutting the margin in the region of the genal angles.

The two associated pygidia are diamond-shaped in outline, about one and a half times as wide as long. The axis is wide, convex and nearly parallel sided with traces of four, possibly five, axial rings and a terminal piece (Pl. 13, fig. 6). The pleural fields are small, triangular and apparently without ribs, apart from the narrow anterior border. Posteriorly the pleural fields appear not to extend as far as the axis, but this is thought to be due to the incomplete preservation of the outer thin portions of the pleural fields, the apparent margin of the pygidium marking the position of the border furrow which must lie close to and parallel to, the actual margin.

Discussion. Although *Plaesiacomia* as currently understood is typically a younger genus, these specimens appear to be better placed here than in *Colpocoryphe* on account of the glabellar outline, lack of lateral glabellar furrows, lack of prominent eye ridges and the absence of a well-developed vincular notch in front of the cephalon. Of the three species currently assigned to *Plaesiacomia*, the Builth specimens are most like *P. rara* from the Caradoc of Bohemia. *P. oehlerti* (Kerforne 1900) differs in its more posteriorly placed eyes and *P.*? *brevicaudata* (Deslongchamps 1825) may be distinguished by the ill definition of the posterior of the pygidial axis and the position of the pygidial vincular furrow.

Family **EOHOMALONOTIDAE** Hupé 1953

Genus ***PLATYCORYPHE*** Foerste 1919

1865 *Homalonotus* (*Brongniartia*) Salter : *pars* 104, 220.
1918 *Eohomalonotus* Reed : *pars* 322.

Diagnosis. With Whittington's (1965*a* : 486) proposed emendations, Whittard's (1961 : 163) diagnosis reads as follows: Cephalon triangular to trapezoidal in outline; glabella sharply truncated anteriorly, trapezoidal; three pairs of straight, sometimes weakly impressed lateral furrows. Facial suture gonatoparian; eyes opposite second or first lateral glabellar lobes; rostral plate axe-shaped, curved connective suture. Hypostoma divided by middle furrow into an anterior lobe much larger than posterior one; no maculae known. Thorax of 13 segments; pleural furrows moderately deep and pleural terminations rounded. Pygidial axis fails to reach posterior margin; pleural fields with up to six ribs which may be furrowed distally.

Type species. *Platycoryphe platycephalus* Foerste.

Distribution. Recently the genus has been recorded from the Arenig of south-western France (Dean 1966 : 318–320). Prior to this, the earliest record was in Britain where the genus ranges from the Lower Llanvirn into the low Caradoc. In Bohemia it is restricted to the Letna Beds of early Caradoc age, whereas in N. America the genus ranges through rocks of ?Trenton to Richmond age and possibly even into the Lower Silurian (see Whittington 1965*a* : 488). The genus may also be present in the Caradoc of south-eastern Turkey (Dean 1967 : 120).

Discussion. The genus has recently been reviewed by Whittington (1965*a*) and no further discussion is necessary.

Platycoryphe vulcani (Murchison)

(Pl. 14, figs. 3–7)

1839 *Asaphus? Vulcani* Murchison : 663, pl. 25, fig. 5.
1854 *Homalonotus* (*Asaphus*) *Vulcani* (Murchison) : pl. 2, figs. 3, 4.
1961 *Platycoryphe vulcani* (Murchison); Whittard : 163–167, pl. 22, figs. 8–19. Includes full synonomy.
1961 *Platycoryphe vulcani* (Murchison); Dean : 343–344.
1965*a* *Platycoryphe vulcani* (Murchison); Whittington : 488.
1966 *Platycoryphe vulcani* (Murchison); Dean : 318–320.

Diagnosis. *Platycoryphe* with cephalic axial furrows straight or slightly convex outwards; posterior glabella width one and three-quarter times anterior width; lateral glabella furrows commonly weakly developed; fossulae absent; paraglabellar area may or may not be developed. Pygidial ribs unfurrowed.

Neotype. GSM. 87137. Enrolled specimen from the Lower Llanvirn Weston Shales, near Curscote, Shropshire. Designated and figured by Whittard (1961 : 166, pl. 22, figs. 8–11).

Locality and horizon. Exposures on the left bank in the ravine in the upper reaches of the Camnant Brook immediately north of the prominent " S " bend 230 yards S. 13° W. of the fence crossing near the stream source; coarse siltstones weathering to rotten stone of Lower Llanvirn age.

Figured material. It. 2832 (Pl. 14, figs. 3, 6); It. 2833 (Pl. 14, fig. 7); It. 2835 (Pl. 14, fig. 5); It. 2836 (Pl. 14, fig. 4).

Description. One cranidium, two librigenae and four pygidia are known from the Lower Llanvirn of the Builth district which appear to be conspecific with the form occurring in the passage beds at the top of the Stapeley Shales and in the Weston Beds of the Shelve region.

Although slightly cracked, the glabella of the Builth specimens is trapezoidal in outline as in the Shelve specimens, the posterior width being one and three-quarter times the anterior width. The lateral glabellar furrows are extremely weakly developed, but faint traces of three pairs are present. As is commonly found in homalonotids, the axial and occipital furrows are more clearly developed on internal moulds than on external moulds. The axial furrows are nearly straight, with slight outward convexity. The occipital furrow is bowed gently forwards medianly and limits the anterior of the simple, flat, narrow (*sag.*) occipital ring. As in the Shelve material, fossulae are apparently not developed. The precise nature of the preglabellar field, fixi- and librigenae is not determinable in the Builth material but as far as can be seen they are similar to those of the Shelve specimens. There is a slight indication of a paraglabellar area developed on the right fixigena.

The hypostoma and thorax are unknown from Builth.

The pygidium is essentially similar to those from Shelve, with five or six ribs present on the pleural fields and apparently with seven axial rings developed.

The external surface of both the cephalon and the pygidium is covered with a coarse, uniform granular ornament.

Discussion. Since Whittard's redescription of this species (1961 : 164–167, pl. 22, figs. 8–19), both Dean (1961 : 344) and Whittington (1965*a* : 488), while accepting Whittard's use of *Platycoryphe*, have pointed out that in some cases it is very difficult to distinguish between species of *Brongniartella* Reed 1918 and *Platycoryphe* on account of the variation in the development of the lateral glabellar furrows. Such an instance is to be found in *P. vulcani* in which the lateral glabellar furrows may be either well developed or virtually obsolete (see Whittard 1961, pl. 22, figs. 12, 16). Although similar variation is not known in the type species *P. platycephalus* (Foerste 1910) it is present in *P. christyi* (Hall 1860) (see Whittington 1965*a* : 488) and it is believed that *vulcani* was correctly placed in *Platycoryphe* by Whittard. Further support for this is given by the absence of any constriction of the anterior portion of the glabella which is characteristically present in *Brongniartella*. The lateral glabellar furrows are also very weakly developed in *P. convergens* Dean 1966 but since there is only one specimen of this, the earliest described *Platycoryphe*, it is not known if the furrows show any variation in their degree of development.

Whittard, in discussing the affinities of this species, concluded that the three European species, *P. bohemicus* (Barrande 1852), *P. foveolatus* (Prantl & Přibyl 1945) and *P. vulcani* were closely related and distinguishable from one another on their glabellar outlines. Whittington (1965*a* : 488) has since given good reasons for considering *P. foveolatus* as synonymous with *Brongniartella platynotus* (Dalman 1828). Whittard acknowledged the possibility that *P. bohemicus* might be conspecific with *P. vulcani* and Barrande's original figures (1852, pl. 34, figs. 40–42) together with Prantl & Přibyl's subsequent illustrations (1949, pl. 1, figs. 1, 2) show that there is very little difference between these two forms. However, they are from quite different horizons and it is possible that *P. bohemicus* from low in the Caradoc is a distinct morphological type with a slightly wider glabella. Apart from these species, Whittington (1965*a*) recognized *P. platycephalus* (Foerste 1910), *P. christyi* (Hall 1860), *P. dubius* (Savage 1913) and *P. dentatus* Dean 1966 has since been described. *P. platycephalus* and *P. christyi* may be distinguished by the presence of fossulae and better developed lateral glabellar furrows. *P. christyi*, *P. dubius* and *P. dentatus* may be distinguished by the presence of furrows on the pygidial ribs. *P. dentatus* is further distinguished by a distinct step in the axial furrows opposite the second lateral glabellar furrows.

Although *P. vulcani* is superficially like *P. convergens* Dean in the obsolescence of the lateral glabellar furrows it may readily be distinguished from Dean's species by its flatter anterior border, more posteriorly placed eyes and straight anterior glabellar margin.

The Builth material is apparently slightly larger than the Shelve specimens, the cranidium and largest pygidium from Builth being about 13·0 and 11·5 mm. in length respectively, compared with lengths of 11·2 and 10·4 mm. for the largest cephalon and pygidium figured by Whittard. None of the Builth specimens however approaches the size of the large isolate pygidium referred to *Platycoryphe* sp. by Whittard.

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